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Background Scientific Information for Candidate Criteria for Considering Species and Community Properties to be Ecologically Significant

Information scientifique de base pour le choix des critères de détermination des espèces et des propriétés des communautés d'importance écologique

Jake Rice (Editor)

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Abstract

Thirteen background papers on candidate criteria for identifying species and community properties are included in this compilation. The ecological properties addressed include Forage Species, Structure – Providing Species, Keystone Predatory Species, Invasiveness, Rarity, Toxic Phytoplankton, Nutrient Important Species, Culturally – Significant Species, Size Composition of the Community, Cumulative Frequency Distribtion of Abundances of Species in the Community, Balance amoug Tropic Levels, Benthic-Pelagic Coupling, and Resilience. Each criterion-specific section summarizes the ecological feature itself and the arguments and evidence for and against species which had that feature being *particularly* ecologically significant. A bibliography is associated with each section, to allow consultation of the key scientific publications by interested readers. Together the reviews provide the scientific background for selection of criteria to be used in identifying Ecologically Significant Species and Community Properties at the scale of Large Ocean Management Areas

Résumé

Treize documents de travail sur les critères possibles de détermination des espèces et des propriétés de communautés sont inclus dans cette compilation. Les propriétés écologiques étudiées comprennent les espèces fourrage, les espèces servant de structure, les espèces prédatrices clés, le caractère envahissant, la rareté, le phytoplancton toxique, les espèces importantes au plan des nutriments, les espèces importantes au plan culturel, la composition par taille de la communauté, la distribution statistique cumulative de l'abondance des espèces dans la communauté, l'équilibre entre les niveaux trophiques, le couplage benthique-pélagique et la résilience. Chaque section consacrée à un critère résume la caractéristique écologique même et présente les arguments qui appuient ou nient l'importance écologique particulière de l'espèce. Une bibliographie est associée à chaque section afin de permettre la consultation par les lecteurs intéressés des principales publications scientifiques. Globalement, les études fournissent l'information scientifique de base pour le choix des critères à utiliser en vue de déterminer les espèces et les propriétés des communautés d'importance écologique à l'échelle des Zones étendues de gestion des océans.

Introduction

As part of the framework adopted to identify Conservation Objectives for the Large Ocean Management Areas (LOMAs) under the Ocean Action Plan Phase I (OAP – I), it is necessary to identify the species and community properties above the species level in each LOMA that are particularly ecologically significant. These species become one of four types of ecosystem properties which contribute to identifying the final list of Conservation Objectives for each LOMA. The interpretation of "ecologically significant" and the role of these Conservations Objectives are explained in detail in CSAS SAR AS-2006-41.

To ensure rigour and consistency in the identification of Ecologically Significant Species and Community Properties, it was necessary to select scientifically based criteria for the identification and ranking of such species. T Steering Committee of Science experts from all DFO Regions met several times by conference call, and identified 14 possible criteria for that purpose. For each candidate criterion, a background paper was prepared by teams of from one to three experts. Each background paper summarized the ecological feature itself and the arguments and evidence for and against species which had that feature being *particularly* ecologically significant. The authors of the background papers were encouraged to be concise, and not present a major literature review. However, in all cases they were to include a bibliography so that interested readers would be able track the scientific basis for the arguments made in the background paper.

Following peer review at a meeting in September 2006, the background papers were revised to address comments from meeting participants. This Research Document contains the final versions of thirteen of the background papers, and a short rationale for considering community properties above the scale of individual species. (Paper 6, on Energy Sequestering Species, was never completed, and was not considered at the meeting.). Only some of the candidate criteria were accepted by the meeting as reasonable criteria for identifying species and community properties as ecologically significant. However, all the background papers are included here, to document to factors which led to each decision to accept or not accept a particular property.

Ecologically and Biologically Significant Species – Forage Fish

K. D. Hyatt

Abstract

Forage species generally consist of small, fish (e.g. herring, sardine, sand launce, capelin etc...) or macro-invertebrates (euphasiids, krill etc...) that occur in local aggregations that serve as an important source of food for many species of fish, birds and marine mammals. Due to generally short life spans, forage species often exhibit rapid numerical responses to changes in either natural or human disturbance regimes (e.g. changes in ecosystem productivity or exploitation respectively). Studies of the role of forage species in marine food webs have repeatedly confirmed that changes to recruitment of forage species may set a cascade of mechanisms in motion that rapidly restructure entire coastal food webs. Historically important commercial fisheries for forage fish species such as herring (Atlantic and Pacific), capelin (Atlantic) and menhaden (Atlantic) have provided sufficiently rich data sets to support active management. However, too little is known of the basic biology, changes in abundance and fisheries for the majority of vertebrate or invertebrate forage species to be actively managed. Forage species exhibit a diverse array of life histories (anadromous coastal, anadromus pelagics, marine coastal, marine pelagics etc...) and habitat requirements (combinations of freshwater, estuarine, marine benthic or marine pelagic spawning). Thus, stock conservation and habitat protection requirements are currently difficult to prescribe beyond general recommendations for the application of either precautionary or adaptive management approaches.

Definition

Forage fish are small, schooling fish or macro-invertebrates which serve as an important source of food for other fish species, birds and marine mammals. However, for brevity, the remainder of the discussion here will be developed around forage fish which are derived from several families (e.g. Engraulidae, Osmeridae, Clupeidae etc...) of small, short-lived species including herring, anchovies, sardine, sand lance and several species of smelt.

Basic Biology

Forage fish are usually composed of species with short life spans and consequently their numeric abundance may fluctuate greatly i.e. they respond quickly to natural factors (e.g. changes in ecosystem productivity or predator abundance) and effects of human disturbance (e.g. habitat degradation and/or fishing). Abundance levels of many forage species are marked by short periods of exceptional abundance followed by lengthy periods of lesser abundance (Bargmann 1998).

Importance

Many species of fish feed on forage fish. For example major predators of herring include Pacific cod (42% of diet), whiting (32%), lincod (71%), halibut (53%, coho (58%) and chinook (58%), (Healey 1980, Gearin et al. 1994, Environment Canada 1994). Sand lance and anchovies (Beacham 1986) are also important sources of food for fish. Similarly anadromous species of forage fish such as shad or eulachon serve as key sources of food for larger, longer lived species such as sturgeon or salmon in estuaries and major river systems respectively (McCabe et al 1993, Stewart et al. 1981). Many species of seabirds depend heavily on forage fish for food and reproductive failures of fish-eating marine birds have been associated with the disappearance of their prey resources (Springer et al. 1984, Monahan 1992). In nearshore environments of the eastern Pacific juvenile herring are probably the most important prey of seabirds (Hay et. al 1989). Sand lance are also important and are the dominant food items for nesting auklets (Bertron and Kaiser 1993). The availability of anchovies directly affects the breeding success of pelicans, terns, gulls and auks (Pacific Fishery Management Council 1996). Marine mammals prey heavily on forage fish; 32 % of the diet of harbor seals in British Columbia is composed of herring (Environment Canada 1994). Forage fish (especially herring and smelt) are an important component of the diet of many marine mammals including: harbor seals, California sea lions, Stellar sea lions, harbor porpoises, Dall's porpoises, Minke whales and humpback whales (Calambokidis and Baird 1994, Graham Ellis –DFO, 2006 pers. comm.).

Because of the importance of forage fish species to many other species, changes in the distribution or abundance of forage fish can have wide ranging impacts on fish, mammals and birds at higher trophic levels . Thus a few species of forage species such as herring, capelin, sand lance, sardines, smelt and menhaden are often positioned in the middle of food-webs supporting important recreational or commercial fisheries for species at higher trophic levels. Modeling studies have suggested that variability in these ecosystems is frequently controlled by variations in mid-level populations of forage species (e.g. Rice 1995). Further, major controls in these ecosystems are not consistently dominated through either "bottom-up" (e.g. Ware and Thomson 2005) or "top-down" effects but rather both "up and down from the middle" (Bakun 1996). Accordingly, changes to recruitment of forage species may set a cascade of mechanisms in motion that rapidly restructure entire coastal food webs (e.g. the herring-cod-marine mammal-seabird food web of the Barents Sea, Hamre 1994 or the mackerel-cod-sand lance and seabird food web of the North Sea, Furness and Ainley 1984, Furness and Camphysen 1997).

Management and Issues

Forage fish frequently exhibit patterns of irregular or spasmodic stock stability (Cady and Gulland 1983) and this has a profound impact on fisheries and resource management. The abundance of forage fish may vary greatly from year to year even in the absence of fishing (Soutar and Isaacs 1974). Fisheries often develop rapidly during periods of exceptional abundance only to decline dramatically when recruitment failures are combined with non-sustainable fishing pressures (e.g. Hourston and Haegele 1980). Further, forage species appear to interact with each other in complex but relatively unpredictable ways which complicates stock forecasting and management (e.g. high abundance of sardine may adversely affect survival and recruitment of herring, Ware and McFarlane 1989). Historically important commercial fisheries for forage fish species such as herring (Atlantic and Pacific), capelin (Atlantic) and menhaden (Atlantic) have provided sufficiently rich data sets to support various forms of active management. However, too little is known of the basic biology, precise changes in abundance and fisheries for the majority of forage fish species to be actively managed. For example, the dynamics of biologically important species such as sand lance, eulachon and the smelt species complex in Canada's Pacific region are known largely in qualitative rather than quantitative terms. Consequently, intensive management of these species and the ecosystems they support is currently not an option. Furthermore, because forage species exhibit diverse life histories (anadromous coastal, anadromus pelagics, marine coastal, marine pelagics etc...) and habitat requirements (combinations of freshwater, estuarine, marine benthic or marine pelagic spawning) stock conservation and habitat protection requirements are difficult to generalize or prescribe.

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Structural Species

Glen Jamieson, Heather Breeze and Tana Worcester

Abstract

"Structural species" create habitat that may be used preferentially by other species and in the marine environment, add to existing physical habitat complexity or create complex habitat in what would otherwise be a homogeneous environment. Some structural species provide physical habitat above the substrate, while others are considered structural due to their role in altering marine sediments, such as through bioturbation. Key structuiral species provide a distinct habitat that supports an associated community. Loss/degradation of this species population would result in loss/degradation of the associated community. Important structural species positively interact with key or characterizing species and are important for their viability. Loss/degradation of these latter species would likely reduce the viability of the key or characterizing species. Criteria to determine key structural species are that the species physically support(s) other macrofauna, and provide either settlement substrate or protection for this associated community, and that it is significantly abundant and spatially distributed in its habitat to influence the overall ecology (e.g., biodiversity) of that habitat. Criteria to determine important structural species are that the species has a significant role in permitting the persistence of key structural species in its accepted habitat, and that it is abundant enough and spatially distributed, or at least potentially so if not impacted by humans, to influence the overall ecology (e.g., biodiversity) of that habitat through its influence on key structural species.

Introduction

"Structural species" create habitat that may be used preferentially by other species. For example, vegetation on land provides both food and structural habitat for many species. This is true in the marine environment as well. However, because of its density, water transports food better than air, and so the marine environment also has sessile animals such as mussels, coral and sponges that also provide structural biogenic habitat. Structure provided by attached or sessile animals is particularly important at depths below the photic zone, where plants cannot survive.

In the marine environment, structural species may add to existing physical habitat complexity or create complex habitat in what would otherwise be a homogeneous environment. In turn, physical habitat complexity has been positively correlated with diversity of reef fishes and some other species (see e.g., Ormond and Roberts 1997; Gratwicke and Speight 2005), higher rates of recruitment of fish in some cases (see e.g., Bell et al. 1987) and higher abundance of certain species (see e.g., Almany 2004; Gratwicke and Speight 2005). Most studies have been carried out in coastal areas or on coral reefs. However, in general complex physical habitats provide a diversity of ecological niches. They may provide shelter or refuge for some species and result in increased food abundance for others (Sebens 1991).

Selected species representative of the importance and biodiversity associated with biogenic structures in the marine environment are: 1) Mussels: variation in richness and diversity through succession is primarily a function of the structural heterogeneity provided by the dominant taxa (structural-heterogeneity hypothesis) (McKindsey and Bourget 2001), 2) Corals: habitat variables that best explained the higher diversity and number of fishes observed were total surface area of rocky shores and the abundance of benthic sessile invertebrates (Ferreira et al. 2001), and 3) Kelps: kelp forests are phyletically diverse, structurally complex and highly productive components of coldwater rocky marine coastlines (Steneck et al. 2002).

Reports have identified other species (e.g., Table 1, Cooke and McMath 2001) that provide obvious physical structure, although their role in the ecosystem as a whole may be less known. Conway et al. (2005) described large sponge reefs on Canada's west coast; Teixidó et al. (2004) referred to sponges, gorgonians, bryozoans and ascidians as "structural species" in an Antarctic benthic community; and numerous reports (e.g. Orth et al. 1984, Willis and Anderson 2003) have documented the role of seagrasses and marine algae in providing structure in coastal environments.

In addition to their role in providing physical habitat, some species may be considered "structural" due to their role in altering marine sediments, such as through bioturbation. Wlodarska-Kowalczuk et al. (2005) refer to large-bodied, deeply penetrating and effective bioturbators, which often act as structural species by maintaining spatial complexity. This role is different from that of species that alter the marine environment through predation (e.g., sea urchins) and in some areas, may play a critical functional role.

The Marine Life Information Network (MarLIN) in the UK has undertaken extensive studies that look at species characteristics and their sensitivities to disturbance, and here we utilize some of the definitions they have adopted. To decide which species best represent the sensitivity of a biotope or community as a whole, they used the following selection criteria (http://www.marlin.ac.uk/glossaries/Sensitive_Species_Criteria.htm):

Rank	Criteria
Key structural	The species provides a distinct habitat that supports an associated community. Loss/degradation of this species population would result in loss/degradation of the associated community.
Key functional	The species maintains community structure and function through interactions with other members of that community (for example, predation, grazing, competition). Loss/degradation of this species population would result in rapid, cascading changes in the community.
Important characterizing	The species is/are characteristic of the biotope (dominant, highly faithful and frequent) and are important for the classification of that biotope. Loss/degradation of these species populations could result in loss of that biotope.
Important structural	The species positively interacts with the key or characterizing species and is important for their viability. Loss/degradation of these species would likely reduce the viability of the key or characterizing species. For example, these species may prey on parasites, epiphytes or disease organisms of the key or characterizing species.
Important functional	The species is/are the dominant source of organic matter or primary production within the ecosystem. Loss/ degradation of these species could result in changes in the community function and structure.
Important other	Additional species that do not fall under the above criteria but where present knowledge of the ecology of the community suggests they may affect the sensitivity of the community.

The criteria used above differentiate between key and important structural species in that key species support an associated community whereas important species influence the viability of key species, such as by keeping parasites, epiphytes, predators or disease organisms at tolerable levels. They also broaden the latter category to include structure of the community in the broad sense, which includes species important to community energy flow patterns and that characterize it taxonomically. An initiative to identify sensitive marine biotopes in the inshore of the Irish Sea used similar definitions.

Because a community is involved, scale of a species' occurrence becomes an issue, both in terms of area of coverage and of density. Relevant data of this type are most available for the intertidal or shallow subtidal, as the extent of these parameters can be seen from the surface and are relatively easily determined. Spatial areas associated with shallow water habitats are likely to be relatively small (in the hundreds of square meters) because the species involved there are greatly affected by exposure to air, wave action and light intensity, and these parameters change rapidly over relatively short depth ranges. In contrast, deeper water species such as deep-water corals and sponges, occur in habitats that are less variable in temperature, salinity and light and are more influenced by currents (food transport) and substrate suitability, all of which are more difficult to measure and differentiate differences in. In such an environment, structural habitats may cover many square kilometers of substrate (e.g. in BC, sponge bioherms cover an estimated 1000 km^2 in four beds in Queen Charlotte Sound).

Criteria to determine ecologically and biologically significant structural species (EBSSs) are proposed as follows:

1. The structural species physically support(s) other macrofauna, and provide either settlement substrate or protection for this associated community. e.g. eel grass beds; macrophyte beds such as kelp, fucus, etc.; mussel beds; sponge reefs; and coral forests or reefs.

2. The dominant species or species type (e.g. sponge) is significantly abundant and spatially distributed in its habitat to influence the overall ecology (e.g., biodiversity) of that habitat.

If important, as opposed to key, structural species are also recognized in this section, then species such as sea otters and even sea urchins could be included here. For example, by preying on herbivores (sea urchins in particular), sea otters permit macrophyte beds to become extensive; in their absence, sea urchin barrens tend to occur, with little kelp present. Since EBSSs are species that require enhanced management, as opposed to normal management, such species could thus include those positive for structural habitat-forming species (these should be conserved) and those negative for structural habitat-forming species (these should be managed to be at a low abundance). Using the above example, since sea urchins have economic value, this has the potential to create conflict, and thus a need for balance by managers. Criteria for these important structural species could then be:

1. The species has a significant role in permitting the persistence of structural species in its accepted habitat.
2. The species is abundant enough and spatially distributed, or at least potentially so if not impacted by humans, to influence the overall ecology (e.g., biodiversity) of that habitat through its influence on actual structural species.

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Table 1: Key structural benthic species identified in Appendix 5 in inshore marine biotopes in the southern Irish Sea (Cooke and McMath 2001).

Fauna: *Mytilus edulis, Ostrea edulis*

Flora: *Corallina oficinalis, Pelvetia canaliculata, Fucus vesiculosus, Fucus serratus, Fucus spiralis, Fucus ceranoides, Enteromorpha* spp., *Sabellaria alveolata, Ascophyllum nodosum, Verrucaria maura, Apistonema carterae, Blidingia* spp., *Laminaria digitata, Audouinella purpurea, Zostera noltii, Zostera marina, Ruppia maritime*

Keystone species: definitions and related concepts in an applied context

Mariano Koen-Alonso and Garry Stenson

Forewords

The designation of Ecologically and/or Biologically Significant Species (EBSS) is one of the tools prescribed for setting Ecosystem Objectives for Large Ocean Management Areas (LOMAs) by Fisheries and Oceans Canada (DFO). The implementation of this tool requires sound operational criteria to identify EBSS. The goal of this working paper is to explore the feasibility of using the keystone species and/or related concepts as one of such criteria. This document is not intended as a thorough review, rather it tries to provide enough up-to-date material to facilitate a productive science-based discussion of the topic.

Definitions

The keystone species concept originated from Paine's work on the rocky intertidal community of the Pacific Coast of North America (Paine 1966). In this system, Paine showed that the starfish *Pisaster ochraceus* controlled the structure and diversity of this community by preying on the competitive dominant mussel *Mytilus californianus*. In the absence of *Pisaster*, mussels out-competed other species like barnacles and benthic algae for the space. These changes and their related effects (e.g. emigration of chitons and larger limpets due to the lack of space and food) reduced the diversity of the community and simplified its structure (Paine 1966). Paine coined the term "keystone" (Paine 1969a) to refer to *Pisaster* and other high trophic status species whose activities disproportionately affect the patterns of species occurrence, distribution, and densities in a biological community (Paine 1969b).

At its inception, the term "keystone species" had a clear (although fairly narrow) trophodynamic meaning: a high trophic level species which, by predation, controls another species that would otherwise dominate the system. In this way, the keystone species effectively determines the structure of the biological community where it is embedded. It is the classical example of top-down control.

The use of term keystone diverged and widened over time. The "keystone species" label has been liberally applied to any species that had a large effect on any aspect ecosystem function (Mills *et al.* 1993). This broadening of the meaning actually weakened the usefulness of the concept, leading to both the suggestion to abandon the label "keystone species" (Mills *et al.* 1993), and the development of its first operational definition (Power *et al.* 1996). Despite their criticism to the use of the term, Mills et al. (1993) highlighted useful aspects of the keystone concept and introduced the idea of community importance, which after some elaboration became a central element in the first "keystone species" operational definition (Power *et al.* 1996).

Power *et al.* (1996) start by distinguishing between dominant and keystone species. Dominant species are the ones which, due to their high abundance, play a major role in controlling the rates and directions of many ecosystem processes. They often provide the major energy flow and/or the three-dimensional structure that supports and shelters other species. On the other hand, a keystone species is one whose effect on its community or ecosystem is large, and disproportionately large relative to its abundance (Fig. 1).

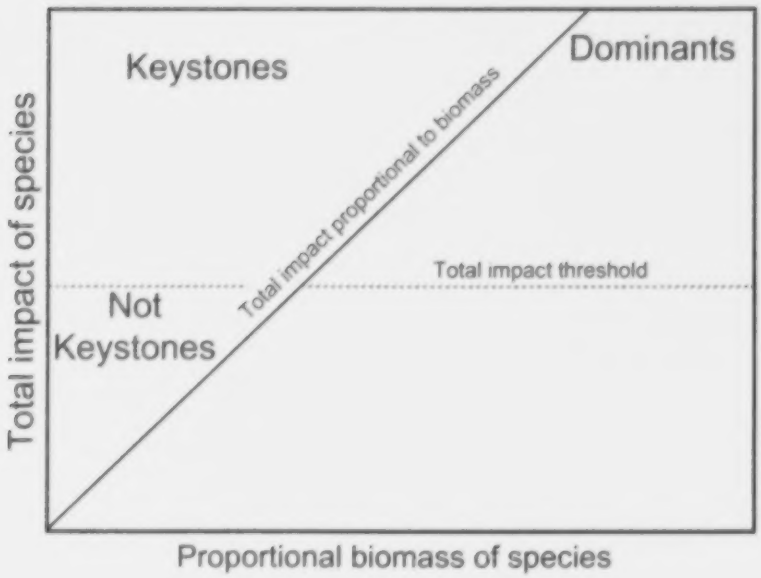

Figure: 1 Schematic representation of keystone and dominant species in the plane defined by the proportional biomass of a species in the community and its total impact on an ecosystem trait. Note that for a species to be considered keystone, its total impact must be large (above some total impact threshold) and it must exceed its proportional abundance by some large factor (i.e. it must lie somewhere above the "total impact proportional to biomass" line). This figure is based on Figure 3 in Power *et al.* (1996).

To make this definition operational it is necessary to measure changes in the community relative to the changes in abundance of a candidate keystone species. Although several alternative and complementary approaches have been used, the most commonly advocated approach to positively link a given species with changes in its community is through an exclusion experiment (Power *et al.* 1996).

Power *et al.* (1996) define Community Importance (*CI*) [of a given species] as the change in a community or ecosystem trait (e.g. productivity, diversity, abundance of a functional group of species) per unit of change in the biomass of the species. In the context of exclusion experiments where the candidate keystone species is completely removed from the system, the community importance can be calculated as

$$CI_i = \left(\frac{x_{before} - x_{after}}{x_{before}} \right) \left(\frac{1}{p_i} \right) \qquad \text{Eq. 1}$$

where CI_i is the Community Importance of species i, x_{before} and x_{after} are the quantitative measures of a community or ecosystem trait before and after the removal of species i, and p_i is the proportional biomass of species i in the whole community before its removal. If the effect of the species on the community or ecosystem trait is directly proportional to its abundance, the CI_i value would be -1 or 1 depending if the effect is positive or negative. If the species is a keystone, the absolute value of CI_i is expected to be much larger than 1 (Power *et al.* 1996).

Power *et al.* (1996)'s operational definition broadens the scope of the concept by allowing keystones species to affect a multitude of ecosystem processes (not just the original trophodynamic effects), but requires them to have large total effects on the community while being relatively low in terms of biomass (Fig. 1).

Although a step forward, this definition also has caveats (Piraino *et al.* 2002;Davic 2003). For example, the keystone designation only can be fully granted after removal experiments to assess the impact on the community or ecosystem trait, provides no *a priori* insight on which species may be considered suitable keystone candidates, and the lack of the original food web focus may still allow for a too broad usage of the concept (Davic 2003). Furthermore, from a management and conservation perspective the conceptual difference between keystone and dominant species is not necessarily relevant since both types of species have large (maybe even identical) effects on ecosystem function (Fig.1), and hence, be equally ecologically significant (Davic 2003).

These issues led Davic (2003) to propose a new operational definition of keystone species which brings back the food web focus, links the keystone and functional group concepts, eliminates the dichotomy between dominant and keystone species, and allows *a priori* identification of potential keystone species. According to Davic (2003), a keystone species is a strongly interacting species whose top down effects on species diversity and competition is large relative to its biomass dominance within a functional group.

The idea behind this definition is that any species that is dominant in biomass within a functional group could potentially regulate species diversity in functional groups from lower trophic levels. It also implies that control of ecosystem processes may be shared by several keystone species acting at multiple trophic levels. Since a keystone species is expected to dominate in biomass within its functional group, potential keystone candidates can be proposed by only examining the composition of functional groups and without the need of calculating the p_i with respect to the entire biological community (this overcomes issues like: do we need to know the total biomass of zooplankton to calculate the p_i of cod?). This definition opens another Pandora's box: how do we identify functional groups? Davic (2003) suggests that functional groups can be assembled by first identifying clusters of species with similar evolutionary histories, and then aggregating these species into feeding guilds by trophic level and foraging behavior [e.g. the granivores, folivores and insectivores rodent feeding guilds identified by Fox and Brown (1993) in their study of a desert ecosystem]. Using this definition the starfish *Pisaster* from Paine's original work will be selected as a potential keystone species because it dominates in biomass the top predator trophic level in its community.

The comparison between Power *et al.* (1996) and Davic (2003) definitions renders some useful observations. Power *et al.* (1996)'s definition emphasizes per unit of biomass effects of a species on its community in order to define a given species as "keystone", while downplays the role of the specific mechanisms which produce the effect (i.e. a keystone species can be involved in top-down, bottom-up, or wasp-waist control). On the other side, Davic (2003)'s definition puts the emphasis on the mechanisms (top-down control of lower trophic level diversity and competition), while dismisses the relative abundance of the keystone species in the whole community. For Davic (2003) it does not matter if the species is proportionally abundant at the whole community level or not, but he suggests that keystone species will be biomass dominants within their functional groups. Furthermore, Davic (2003) makes a clear distinction between "key" and "keystone" species, where a "key species" is one that regulates energy flow/nutrient dynamics of the community. If a species regulates both diversity of lower trophic levels and the energy flow/nutrient dynamics, then it will be "key" and "keystone" at the same time. This is possible because these terms identify process roles of species within ecosystems, and nothing prevents a species from occupying multiple roles (Davic 2003). Despite their differences, these two definitions also have common features. Keystone species are not necessarily top predators but they should be strong interactors within their communities, their total impact on the community must be large, and these impacts are assessed using some quantitative measurement (e.g. the *CI* index).

Paine's original work identified keystone predators, but is also among the first experimental studies which actually show the dependency of community dynamics on both food web structure and the distribution of interaction strengths among its components. In fact, classical keystone predation does not just identify a specific species or a single and strong predator-prey interaction; it is a particular food web configuration with a specific distribution of weak and strong links (i.e. strong predation relative to other high level predators in the system, on a competitive dominant prey) (Menge 1995). This is the reason why *Pisaster* is undoubtedly a keystone species in the context of the wave-exposed system studied by Paine, while it is not in similar but wave-sheltered communities (Menge *et al.* 1994); the keystone role is context and scale dependent.

If, for our purpose here, we simplify reality based on the above discussion, we can state that community regulation emerges from the interplay between food web structure and the distribution of interaction strengths among its components. Some of these components will be strong interactors and may play a more significant role in shaping and controlling community dynamics. Therefore, for the practical issue of identifying EBSS, we may be better off concentrating our efforts on detecting species that have strong trophodynamic effects on their communities, regardless if they formally deserve the key, keystone or dominant labels. We will refer to these species as "key trophic species".

Interaction strength, trophic impacts, and community dynamics

Interaction strength is generally described as the magnitude of the effect of one species on the abundance of another (Berlow *et al.* 1999). For example, if we equate the community or ecosystem trait *x* considered in the *CI* index (eq. 1) to the abundance of a species in the community, this index can be used to measure interaction strength (Berlow et al. 1999), although we should keep in mind that it was originally intended for broader applications (Power et al. 1996).

Four conceptually different approaches have been widely applied to assess interaction strength (Laska and Wootton 1998), but many more different metrics and related frameworks actually used to quantify it (Berlow *et al.* 1999;2004;Wootton and Emmerson 2005). These four common approaches include the community matrix, the Jacobian matrix, the inverse Jacobian, and the removal matrix (Laska and Wootton 1998, see Appendix 1). The community matrix defines the interaction strength as parameters in dynamic models of species interactions. In this case the interaction strength is defined as the average direct effect that a single individual (or unit of biomass) has on a single individual (or unit of biomass) of another species (e.g. the α parameter in Lotka-Volterra competition models). The Jacobian matrix defines the interaction strength as the partial derivative of the growth equation of one species with respect to another evaluated at equilibrium. This interaction strength refers to the direct effect of one individual (or unit of biomass) of one species on the total population of another species at equilibrium. The inverse Jacobian matrix defines the interaction strength as the negative inverse of the Jacobian matrix. The inverse Jacobian matrix summarizes the outcomes of all press perturbation experiments (see Appendix 1 for details), and describes the total direct and indirect effects on one species as a result of a constant removal or addition of another species (Bender *et al.* 1984;Yodzis 1988). The removal matrix represents an empirical viewpoint where the interaction strength is defined as the difference between the equilibrium abundance (or biomass) of a given species before and after the removal from the community of another species (e.g. Paine 1992). Like the inverse Jacobian, the removal matrix also considers all direct and indirect effects of removing one species from the system. However, they differ in the sense that the removal matrix does not have any particular mathematical meaning but it represents exactly what empiricists measure, and unlike the inverse Jacobian, it also considers the structural changes in the food web resulting from the removal of a species (Laska and Wootton 1998).

Among these four common approaches, the first two measure interaction strength as a property of the individual link (i.e. direct effects), while the last two consider the effects traveling through all the paths in the food web that connect the two species (i.e. direct and indirect effects). For the purpose of detecting key trophic species in the food web, metrics that consider both direct and indirect effects would be preferable.

Although less present in the mainstream literature on interaction strengths, another metric that also considers direct and indirect effects of trophic interactions is the Mixed Trophic Impacts (MTI) matrix (Ulanowicz and Puccia 1990, see Appendix 1). This metric, originally derived from economic input-output analysis, is currently incorporated in the Ecopath with Ecosim (EwE) software, and lies at the core of a recently proposed method for identifying keystone species in food web models (Libralato *et al.* 2006).

All three approaches that consider direct and indirect effects (inverse Jacobian, removal matrix and MTI) render a single pairwise value which characterizes the interaction between a pair of individual species. If we want to identify key trophic species at the community level, we will need to summarize the effect of each species onto all the others.

Based on the MTI matrix and considering that mixed trophic impacts m_{ij} can be positive or negative (see Appendix 1), Libralato *et al.* (2006) defined the overall effect of one species onto all others as

$$\varepsilon_i = \sqrt{\sum_{i \neq j}^{S} (m_{ij})^2} \qquad \text{Eq. 2}$$

where the m_{ij} are the pairwise mixed trophic impacts, and *S* is the total number of species in the food web model. They use this metric to estimate the *CI* index (eq. 1) as

$$CI_i = \varepsilon_i \frac{1}{p_i} \qquad \text{Eq. 3}$$

where p_i is the biomass proportion of species *i* in the whole system. They attempted to use this equation to identify keystone species *sensu* Power et al (1996). After some exploration they suggested that eq. 3 weighed p_i too heavily and settled for

$$KS_i = \log[\varepsilon_i (1 - p_i)] \qquad \text{Eq. 4}$$

where KS_i is their proposed "keystoneness index". Using eq. 4 they identified as keystone those species with the highest KS_i values. Considering an Ecopath model for the Newfoundland shelf (Bundy 2001), the top ten species in the keystoneness spectrum were cetaceans, capelin, harp seals, hooded seals, large zooplankton, adult Greenland halibut, bivalves, Pollock, juvenile Greenland halibut, and phytoplankton (Libralato *et al.*2006).

The rationale behind the use of eq. 3 or 4 (Libralato *et al.* 2006) highlights the question of how species abundance must be treated when calculating its impact on the community. Both inverse Jacobian and Removal matrix approaches consider densities explicitly; the output of these analyses are theoretically expected or observed changes in equilibrium densities. For this reason, if these methods were to be used in conjunction with something like eq. 2, the pairwise interaction strengths will need to be standardized. On the other hand, MTI is based on proportional input and output flows and the effect of the actual abundance is essentially factored out. This has been pointed out to explain the higher agreement between the total impacts evaluated by the inverse Jacobian and dynamic models when compared with MTI assessments (Loengarov 2004).

Inverse Jacobian and Removal matrix approaches assume equilibrium conditions, while MTI *per se* do not necessarily requires this assumption. However, steady-state models are usually the only source for the flow estimates needed for MTI (e.g. EwE models, Libralato *et al.* 2006), making in practice this last approach as dependent as the others of equilibrium assumptions. Assuming equilibrium seems an odd proposition; most exploited ecosystems are quite likely very far from this state. However, for the purpose of identifying key trophic species this may not be such a serious issue. As always, the devil is in the details. If the results from the modeling exercise appear a reasonable representation of how the system may have looked like under equilibrium or near equilibrium conditions, then identifying key trophic species from them is a worthwhile endeavor. If the steady-state picture seems questionable, so will be any key trophic species identified from it. We should keep in mind that modeling results will always be as good as the data we put in them. If highly aggregated functional groups and/or poorly studied species emerge as key trophic species from these analyses, a healthy skepticism about the result must kick-in. They may be correct, sometimes topology alone may help to identify key trophic species (see below), but a closer examination is certainly called for. Probably the most serious issue of using equilibrium models in this context is the fact that they cannot detect multiple basins of attraction. Theoretical press perturbation experiments assume the existence of a single equilibrium point from where the system is moved away by small enough perturbations (Bender *et al.* 1984;Yodzis 1988;1996;1998). If real systems have distinct regimes (i.e. distinct and persistent food web [dynamic]

configurations), it is reasonable to expect that the role of key trophic species may be played by different biological species in each regime.

The removal matrix approach will eliminate many modeling-related caveats. It implies an experimental setting; the consequences of removing a given species are directly measured. However, real exclusion experiments are possible in a relatively limited set of scenarios and pose a large number of logistical issues. Still, if carried out properly, they can provide strong evidence about interaction strength and trophic impacts in real communities (Paine 1992;Wootton 1997).

One solution is the combination of modeling work with careful exploration of the uncertainties involved. Using bionergetic-allometric models and the inverse Jacobian approach, Yodzis (1998) evaluated how the uncertainty in key parameters of the model affected the assessment of the impact of fur seals on commercial species. The explicit incorporation of uncertainties into the process of estimating interaction strengths and identifying key trophic species is a necessary step, and the feasibility of its implementation is certainly not constrained to the inverse Jacobian approach.

In real communities, the distribution of interaction strengths among species appears to be biased towards weak interactions (e.g. Paine 1992, Wootton 1997). This distribution is clearly non-random and has important stability implications (e.g. de Ruiter *et al.* 1995). Strong predator-prey interactions in dynamic models usually produce highly oscillatory or chaotic behaviors. However, if these strong interactions are embedded in a matrix of weak ones, these weak links can act as dampeners or inhibitors of the oscillatory sub-systems, promoting the stability of the whole system (McCann *et al.* 1998). As McCann et al. (1998) said "it seems, then, that weak interactions may be the glue that binds natural communities together". Given our goal of detecting key trophic species, it is even more important to keep in mind the role of weak links, because without them (e.g. impoverished food webs) the average interaction strength may tend to increase, and hence hindering system stability.

Having said this, it is also true that the elimination of key trophic species will most certainly have serious consequences on system dynamics. For example, a recent study based on the topology of three highly resolved real food webs showed skewed distributions of connections (Solé and Montoya 2001). If we consider the number of connections of a given species as a sort of "topological analog" of interaction strength, then these distributions indicate that few species had many connections ("strong interaction strength") while most of them had only few connections ("weak interaction strength"). Solé and Montoya (2001) also found that these food webs showed high homeostasis to random removal of species, but they were extremely fragile (e.g. very high rates of secondary extinctions) when the removals were directed to the highly connected species. These key trophic species were found at all trophic levels (Solé and Montoya 2001).

Top predators are not the only ones that can be key trophic species, but they can be particularly important in bringing stability to trophodynamic systems due to their capacity of linking [out-of-synchrony] otherwise spatially isolated food web subsystems (McCann *et al.* 2005), and their role as ecological buffers of some environmentally driven patterns (Sala 2006).

Concluding remarks: scientific knowledge, management context and research needs

Labeling a species as keystone, key or any other formal scientific denomination will always be subject to criticism and revision. This is a very good thing; science works by trying (and succeeding) in proving itself wrong. Unfortunately, modifying legislation or formal management procedures and institutions is far more difficult and cumbersome than reviewing our own scientific ideas. Since EBSS is a management tool, we should provide science-based criteria which are as independent as possible from excessively formal definitions while remain strongly attached (and faithful) to scientific facts and/or robust theories.
Although definitive and absolute definitions of keystone predator or interaction strength may remain elusive, there is enough empirical evidence and theoretical support to state that real food webs systems can be described as non-random networks where the distribution of connections between species, and the strength of these links tends to be biased towards few connections per species and relatively weak links. Among these species, those that are highly connected and/or have strong interactions are likely to be the ones that provide

the basic structural integrity of the food web. Seriously harming these key trophic species would likely compromise the whole ecological system, but their conservation in isolation will not ensure its integrity either. The network of weak links in which these species are embedded may play a significant role as a source of stabilizing mechanisms.

If we can accept the above statements, then those species that we refer here as "key trophic species" must be designated EBSS. Proving that a given species actually is a key trophic species is likely to be extremely difficult. Reversing the burden of proof (i.e. every species is a key trophic species until proven otherwise) will not help either; if every species is a key trophic one, and consequently EBSS, none of them are. However, under the umbrella of the precautionary principle, it is reasonable to suggest that any **potential** key trophic species should be granted EBSS status until proven otherwise. The previous sections provide us with enough elements to outline possible protocols to identify "potential key trophic species" (Appendix 2).

In any case, it is important to highlight that the robustness of the results will strongly depend on the kind, quantity and quality of the data available. Less robust analyses can still render candidate EBSS, but the odds of making a mistake will be higher. Designating EBSS to a species which is not a key trophic one will not pose serious conservation issues. However, failing to protect a real key trophic species can have dramatic ecosystem consequences.

Reliable identification of key trophic species depends heavily on information about abundance/biomass and diets composition. DFO capacity to carry-out its standard bottom trawl surveys has been diminished in recent years, and in many regions there is no proper coverage of non-commercial and/or pelagic species. Furthermore, most DFO monitoring programs do not include food habits studies as part of the standard surveys. If we want EBSS to become a truly useful tool and not just a box-checking exercise, we need to address these basic research needs promptly. We may still get away with today's advice using the information collected in the past, but this situation will not hold for long. Everyday that passes leaves us with less and less real data to support tomorrow's advice.

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Appendix 1. Nuts and bolts of some commonly used approaches to measure interaction strength
General approaches described by Laska and Wootton (1998)

Consider a multispecies dynamic system of *S* species with population dynamics equations for each species defined by

$$\frac{dN_i}{dt} = f(N_1,...,N_i,...,N_S) \equiv f_i \qquad \text{App.1}$$

where N_i is the density of species *i* and f_i describes the population growth of species *i* as a function of all population densities in the community.

The following interaction matrices will be *S*x*S* matrices where rows and columns are related to the corresponding species. Each element in these matrices will be denoted by the subindices *i* (row) and *j* (column). The ij^{th} element represents the effect of the species *j* onto species *i*.

1. **Community matrix (M)**

   Each element in this matrix is defined by

$$M_{ij} = \frac{\partial\left(\frac{1}{N_i} f_i\right)}{\partial N_j}$$

2. **Jacobian matrix (A)**

   Each element in this matrix is calculated at equilibrium ($\mathbf{N}^* = \{N_1^*,...,N_i^*,...,N_S^*\}$) and defined by

$$A_{ij} = \left.\frac{\partial f_i}{\partial N_j}\right|_{\mathbf{N}^*}$$

3. **Inverse Jacobian matrix ($-\mathbf{A}^{-1}$)**

   Although named after the method employed to calculate it, it makes more sense to present the elements of this matrix in terms of the quantity of interest.

   A press perturbation experiment consists in adding a constant (positive or negative) input to any species *j* (I_j) in the multispecies dynamic model defined by App.1. This means that the population growth of *j* is perturbed from the original $\frac{dN_j}{dt} = f_j$ to $\frac{dN_j}{dt} = f_j + I_j$. Once perturbed, the system is allowed to achieve a new equilibrium, measuring then the changes in all equilibrium densities with respect to the perturbation (Bender *et al.* 1984; Yodzis 1988;1996;1998).

If we assume the existence of an equilibrium point for the original system, and the perturbation [input] I_j is small enough to move the system only slightly away from it, then the change in the equilibrium value of any species i (N_i^*) with respect to I_j is

$$\frac{\partial N_i^*}{\partial I_j} = -\left(\mathbf{A}^{-1}\right)_{ij}$$

where $\mathbf{A}^{-1}$ is the inverse of the Jacobian matrix (**A**) calculated at equilibrium.

4. **Removal matrix (R)**

Each element of this matrix is calculated as the difference of two equilibrium densities as

$$R_{ij} = N_i^*(\text{all species present}) - N_i^*(\text{species } j \text{ removed})$$

Mixed Trophic Impacts (MTI) approach developed by Ulanowicz and Puccia (1990)

The MTI approach is based on the balance between fluxes of biomass/energy coming in and out of the components in a food web model. It defines the net impact of a species i onto another species j as

$$q_{ij} = g_{ij} - f_{ji}$$

where q_{ij} is the net impact of i upon j, g_{ij} is the proportion in the diet of j constituted by i (i.e. the positive effects that i exerts on j by being a source of food), and f_{ji} is the fraction of the net output (i.e. total production minus respiration) of j that goes to i (i.e. the negative effects that i exerts on j by being its predator). q_{ij} is bounded between -1 and 1. For well resolved food webs, either g_{ij} or f_{ji} are expected to be zero in most cases.

These q_{ij} can be arranged in a matrix **Q** which contains all possible pairwise net impacts. These net impacts only evaluate direct effects between each pair of species.

Following standard input-output analysis, the MTI approach assumes that the indirect effect traveling through a given path can be calculated as the product of all the q_{ij} in the path (i.e. $p_{iz} = q_{ij}q_{jk}...q_{yz}$), and that the total direct and indirect effects between two species can be calculated as the summation over all distinct paths that connect them (i.e. $m_{iz} = \sum_{l=1}^{L} p_{iz,l}$ where L is the total number of distinct paths connecting species i and z). In this way, the mixed trophic impact between species i and j (m_{ij}) can be calculated; m_{ij} considers all direct and indirect effects. All these m_{ij} can be arranged in a matrix of trophic impacts **M**. Furthermore, this matrix of mixed trophic impacts can be calculated from **Q** as

$$\mathbf{M} = (\mathbf{I} - \mathbf{Q})^{-1} - \mathbf{I}$$

where **I** is the identity matrix.

Appendix 2. Illustrative straw-man protocol to identify key trophic species

This is a schematic protocol for identifying key trophic species. It is only intended as an illustration of how a real one may look like. Its goal is to stimulate discussion; it does not constitute a proposal.

1. Which type of information is available about the biological community?

   a. Nothing ..... *Go to 2*
   b. Estimates of abundance/biomass and literature information about food habits ..... *Go to 3*
   c. Good, but only qualitative, diet matrix ..... *Go to 4*
   d. Estimates of abundance/biomass and a quantitative diet matrix ..... *Go to 5*
   e. Time series of abundance/biomass and diet composition ..... *Go to 6*

2. You do not know enough; you are in deep trouble.

   a. Start research programs urgently.
   b. If you managed to get abundance/biomass information and some general diets ..... *Go to 3*
   c. If you managed to get reasonable, but qualitative, diet data ..... *Go to 4*
   d. If you managed to get abundance/biomass and good diet information ..... *Go to 5*

3. You are in a weak position.

   a. Use the available diet information to build a food web diagram for the system.
   b. Based on the food web diagram and the biological knowledge of the species, build functional groups *sensu* Davic (2003).
   c. Using the estimates of biomass for the species and the functional groups defined in 3.b. calculate the p_i for the species in each functional group.
   d. Identify the functional groups which are dominated by one or very few species; these species are your "potential key trophic species" and candidate EBSS.
   e. Start diet monitoring programs and continue with the abundance/biomass surveys.
      Once you gather enough diet data ..... *Go to 5*

4. You are in a weak position

   a. Use the diet information to build a detailed food web diagram.
   b. Calculate topological indices and the frequency distribution of connections (e.g. Solé and Montoya 2001).
   c. Identify those species with high number of connections; these species are your "potential key trophic species" and candidate EBSS.
   d. Start abundance/biomass survey programs and continue with the diet monitoring program.
      Once you gather enough abundance/biomass data ..... *Go to 5*

5. You are in a reasonable position.

   a. Perform the analysis detailed in 3 and 4.
   b. Combine diet and biomass data to build static models (e.g. Yodzis 1998, Ecopath). Remember that these models will assume equilibrium; their purpose here is to identify key trophic species, not to predict system dynamics.
   c. Use these models to calculate mixed trophic impacts (MTI) (Ulanowicz and Puccia 1990) and the inverse Jacobian matrix (e.g. Yodzis 1998). Summarize results for the whole system (e.g. Libralato et al. 2006).
   d. Explore the robustness of the results obtained in 5.c. by exploring model uncertainty (e.g. Yodzis 1998).
   e. Compare the results from all analyses. The key trophic species identified so far are your EBSS candidates. If the results among approaches mainly agree, you have a reasonably robust set of candidates. If the results among approaches differ in some significant way, you

must implement specifically directed research to resolve the controversy. There is something fishy that needs to be addressed.

f. Continue with the diet monitoring program and the abundance/biomass surveys. When you have a reasonable diet time series ..... Go to 6

6. You are in a very good position; you are the envy of your peers.

   a. Perform the analyses detailed in 5.
   b. Develop multispecies dynamic models (e.g. McCann et al. 1998), or appropriate time series analyses.
   c. Compare the results from all analysis. Pay particular attention to species that may have played key trophic roles in different moments in time. If the system has multiple domains of attraction, it is quite possible that each system configuration is characterized by different key trophic species. If there are documented regime shifts for the system under consideration, the search for regime-dependent key trophic species is particularly important.
   d. Continue with the diet monitoring program and the abundance/biomass surveys.

Invasiveness as a Criterion for Identifying Ecologically Significant Species

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Abstract

Invasiveness is an important criterion for identifying Ecologically Significant Species because historical data confirm that invasive species can have a controlling influence on key parts of ecosystem structure and function. Invasives are marine or freshwater animal species, or aquatic plant species that have been introduced or could potentially be introduced into a new aquatic ecosystem, that cause or potentially cause harmful impacts to the natural resources in the native aquatic ecosystem and/or the human use of the resource. The potential controlling influence of invasive species on ecosystems can be determined using standardized risk assessment procedures. Under the invasiveness risk criterion, species that score high or medium for probability of establishment and high or medium for consequences of establishment will be categorized as an Ecologically Significant Species that requires enhanced management. Currently, both intentional (proposed) and unintentional introduced species are managed by DFO under the National Code on Introductions and Transfers of Aquatic Organisms, and the National Action Plan to Address the Threat of Aquatic Invasive Species, respectively. Using invasiveness as a criterion for Ecological Significance ensures that enhanced management and control of invasives is explicit in setting Conservation Objectives, and it is consistent with existing DFO programs.

Background

Ecologically Significant Species (ESS) are selected priority species that require enhanced management for protection or control, while allowing sustainable activities to be pursued where appropriate. Criteria for selecting ESS must be based on consistent standards and must be science-based.

Criteria for identifying Ecologically and Biologically Significant Areas (EBSA) have already been selected (DFO 2004). Ocean areas were designated 'significant' because of the functions they serve and/or because of structural properties. Further, areas were evaluated with regard to their significance along five dimensions, namely Uniqueness, Aggregation, Fitness Consequences, Resilience and Naturalness.

Invasive species, one of several candidate criteria for determining significance, are evaluated below first by acknowledging the potential influence of aquatic invasive species (AIS) on ecosystem structure and function (via risk assessment) and secondly by considering the five EBSA dimensions in the context of ESS and invasive species.

To protect native species and biodiversity, invasive species require enhanced management in the form of proactive control measures.

Management of Invasive Species by DFO

To deal with threats posed by invasive species, the Canadian Council of Fisheries and Aquaculture Ministers (CCFAM) developed two task groups, the Introductions and Transfers Task Group and the Aquatic Invasive Species Task Group. The management of authorized introductions, such as aquaculture and fish stocking, was covered by the Introductions and Transfers Task Group (CCFAM 2003), and the prevention of accidental introductions were covered by the Aquatic Invasive Species Task Group (CCFAM 2004). Both CCFAM task groups were responsible for developing management plans designed to protect natural ecosystems from the harmful impacts of invasive species, to be consistent with the UN Convention on Biodiversity and the Canadian Biodiversity Strategy. Both accidental and intentional introductions may involve invasive species (potentially) and therefore are relevant to ESS.

Managing accidental introductions is problematic because there are many potential vectors of introductions, and the pathways are sometimes unknown or unanticipated. Invasive species were defined by CCFAM as non-indigenous species that cause or potentially cause harm to native aquatic ecosystems and/or the human use of the resource (below). The goal of the Canadian Action Plan to Address the Threat of Aquatic Invasive

Species was to prevent the introduction of harmful AIS and to remediate the impact of those already in Canada. Prevention is achieved by managing the key known vectors of introduction (ballast water, live bait, aquarium trade, and others).

For intentional introductions, the goal of the National Code on Introductions and Transfers of Aquatic Organisms (I&T Code) is to address concerns of transfers by providing a standard risk assessment process that can be applied across all jurisdictions. The I&T Code recognizes that there are social and economic benefits derived from fish stocking and culture, but also if there is an unintentional release, and if the species is invasive, then the consequences of establishment to native ecosystem structure and function can be negative.

Risk Assessment

Risk assessment is the process of identifying a hazard, and estimating the risk presented by the hazard, in either qualitative or quantitative terms (CCFAM 2003). Invasive species are a key threat to aquatic ecosystems, fisheries resources, fish habitat and aquaculture.

The qualitative risk assessment framework included in the I&T Code assesses risk of intentional introductions in three main steps: 1) probability of establishment, 2) consequences of impact (i.e., magnitude of impact), and 3) a final risk assignment. Ecological, genetic and parasite/disease risks are addressed. The framework in a condensed form is given in Appendix II. The first step explicitly evaluates 'invasiveness', the likelihood that a species will survive in a new environment and the potential range expansion, given its life history traits and habitat preferences. The final risk assignment is cautionary – if either the probability of establishment or the consequences of impact is high, the final assignment is high (Appendix II, part 3). Likelihood of establishment and magnitude of impact are key criteria for identifying significant invasive species that require enhanced management.

The DFO Centre of Expertise for Aquatic Risk Assessment (CEARA) was established in 2006 to develop national standards for conducting biological risk assessments of AIS not authorized for introduction, and to prioritize risk assessment needs.

A recent example of a risk assessment was for the grass carp (*Ctenopharyndon idella*), a non-indigenous species which, because it has a herbivorous diet, was proposed for biological control of macrophytes in drainage ditches in Alberta. Because of the high probability of establishment (including a large area of potential expansion), and because of its potential negative impacts on biodiversity, this species was assessed as high risk (DFO, 2004). Mitigation controls were recommended.

Risk assessments are currently underway for several marine species, including tunicates (5 species), *Codium fragile*, and *Carcinus maenas* (A. Locke and M. Koops, pers. comm.). The goal of ongoing CEARA research is to develop quantitative risk assessment frameworks (N. Mandrak and M. Koops, pers. comm.).

Links with Criteria Used for Determining Significant Areas (EBSA)

As noted in the Background, five characteristics or dimensions were used to evaluate the significance of EBSAs, each based on the functions and/or structural properties they served in the ecosystem. That is, 'significance' refers to the role of a species, habitat, community attribute or specific area in the ecosystem. The five properties are: uniqueness, aggregation, fitness consequences, resilience and naturalness. Although these properties were used as descriptors of significant areas, some are valid and relevant for identifying significant species as well. Invasive species that impact and disrupt in a significant manner the structure and function of natural ecosystems can be viewed as a significant species that require enhanced control.

Impacts of four invasive taxa found in Canada were reviewed for evidence that these taxa affected native ecosystem structure and function. The four taxa were 1) *Didemnum* sp. (tunicate); 2) *Petromyzon marinus* (sea lamprey); 3) *Dreissena polymorpha* (zebra mussel); and, 4 *Carcinus maenas* (green crab). All four taxa

are listed among the top 100 invasive species in the IUCN invasive species database. Details of impacts (Table 1) were obtained from the IUCN synposis for each species (www.issg.org/database).

Uniqueness:

defined as 'areas whose characteristics are unique, rare, distinct and for which alternatives do not exist' (DFO 2004). No examples of disruption of unique habitats were found in the IUCN synopses for these invasive species. However, uniqueness could apply to biota as well as areas. Invasive species are unique genetically, and thus negatively affect natural biodiversity by their occurrence.

Aggregation: 'areas where most individuals of a species occur for some part of a year, or where most individuals use the area for an important function in their life history'.

An example of invasive disruption are sea lamprey, which target large salmonines as parasitic prey (IUCN synopsis) when they aggregate for feeding.

Aggregation can also apply to aquaculture: two of the invasive species (*Didemnum sp.* and *C. maenas)* are of particular concern because of the threats they posed to the mollusc aquaculture industry (aggregation of cultured species).

Fitness Consequences: 'areas where life history activities make a major contribution to the fitness of the population or species'.

If invasive species become established, many of these species can have a significant effect on fitness of native species in specific habitats. All four species impacted on fitness during different life history stages; the function impacted was species-dependent (Table 1).

Elsewhere, as evidence of their influence on fitness, invasive species are listed as a key threat to many at-risk species listed under the Species at Risk Act (SARA) (Dextrase and Mandrak 2006).

Resilience: 'areas where the habitat structures or species are highly sensitive, easily perturbed, and slow to recover'.

Resilience of ecosystems was discussed in the IUCN synopsis of *Didemnum*. Although this invasive taxon is observed primarily colonizing artificial substrates in harbours and manmade structures, there are concerns that natural reefs may become vulnerable as well. Many reefs are becoming degraded due to anthropogenic activities, and resilience of these ecosystems is decreasing. Colonization by *Didemum* would further decrease resilience by decreasing biodiversity.

Naturalness: 'areas that are pristine and characterized by native species'.

Negative impacts on biodiversity and community structure were documented for all four invasive species (Table 1). For example, *Dreissena polymorpha* have displaced native mussels in the Great Lakes, and have shifted nutrient balances from the pelagic to the benthic zone. Impacts on naturalness by invasive species are well documented, providing strong support for invasive species as a key criterion for determining significance.

Conclusion: Invasiveness is an important criterion for determining Ecologically Significant Species

Invasiveness should be used as a criterion for identifying Ecologically Significant Species that require enhanced control because these species can have a controlling influence on the structure and function of ecosystems. Historically, invasive species have negatively impacted on the life history functions (spawning, nursery, feeding, refugia, and migration) of various native or cultured species and they have impacted on the structural properties of ecosystems (macrophyte beds, biodiversity). The transfer of aquatic organisms from one ecosystem or region to another, both deliberate and accidental, is ongoing and increasing. Currently, planned transfers (aquaculture, fisheries, other) and unplanned transfers are being managed by the

implementation of risk assessment procedures. A designation of high or moderate risk indicates a species is invasive and that elevated management actions (controls) are needed. In this context, invasive species as a criterion for ESS differs from the other criteria; the management action is for control (prevention of introduction) rather than protection of the species, although the ultimate goal is the same (i.e., conservation of biodiversity). Inclusion of invasive species as a criterion for ESS is consistent with the ongoing risk assessment and management of invasive species in DFO, and would make the influence of these species explicit when setting Conservation Objectives for Large Ocean Management Areas.

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Table 1. Examples of potential impact of invasive species on function and structure of ecosystems. The invasive species evaluated were 1) *Didemnum* sp.; 2) *Petromyzon marinus*; 3) *Dreissena polymorpha*; and 4 *Carcinus maenas*. Information on impacts were obtained from the IUCN synposis for each species (www.issg.org/database)

	Uniqueness				Aggregation				Fitness Consequences				Resilience				Naturalness			
Species	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Function																				
Spawning									√	√	√	√								
Nursery																				
Feeding										√	√									
Refugia						√				√?	√									
Migration										√										
Structure																				
Macrophytes											√									
Reefs					√?				√				√				√			
Biodiversity							√				√				√		√	√	√	√

Appendix I

Definitions:

Aquatic invasive species:

Fish, animal, and plant species that have been introduced into a new aquatic ecosystem and are having harmful impacts on the natural resources in the native aquatic ecosystem and/or the human use of the resource (CCFAM 2004).

Hazard:

A thing or an action that can cause adverse effects (CCFAM 2003).

Invasive Species (nuisance or pest species):

A non-indigenous species the introduction of which into an ecosystem may cause harm to the economy, environment, human health, recreation, or public welfare (CCFAM 2004).

Intentional Introduction:

The deliberate release, or holding, of live aquatic organisms in open-water or within a facility with flow-through circulation or effluent access to the open-water environment outside its present range (CCFAM 2003).

Risk:

The probability of a negative or undesirable event occurring: the likelihood of the occurrence and the magnitude of the consequences of an adverse event; a measure of the probability of harm and the severity of impact of a hazard (CCFAM 2003).

Risk Assessment:

The process of identifying and describing the risks of introductions or transfer of aquatic organisms having an impact on fisheries resources, habitat or aquaculture in the receiving waters before such introductions or transfers take place; the process of identifying a hazard and estimating the risk presented by the hazard, in either qualitative or quantitative terms (CCFAM 2003).

Appendix II. Three steps of a qualitative risk assessment framework (intentional introductions; condensed from CCFAM 2003).

Step 1 Determining the **Probability of Establishment** (beyond the intended area of introduction)

Element	**Probability of Establishment (H, M, L)** [1]	**Level of Certainty (VC to VU)** [2]
Estimate of probability that the introduced species successfully colonizes and maintains a population in the intended area of introduction		
Estimate the probability of its spreading beyond the intended area of introduction or, Estimate the probability of its spreading beyond the intended are of introduction **if it escapes** (apply to cases in which the intended area of introduction is a confined environment)		
Final Rating		

1. H High; M Medium; L Low
2. VC Very certain; RC Reasonably certain; RU Reasonably uncertain; VU Very uncertain

Step 2 Determining the **Consequence of Establishment** of an Aquatic Organism

Element	**Consequences of Establishment(H, M, L)**	**Level of Certainty (VC to VU)**
Estimate of magnitude of environmental impacts, if established.		
Ecological impact on native ecosystems both locally and within the drainage basin.		
Genetic impacts on local self-sustaining stocks or populations.		
Final Rating		

Step 3: Determination of the **final risk** estimate

Probability of Establishment	Consequences of Establishment	Final Risk Estimate
High	High	High
High	Medium	High
High	Low	Medium
Medium	High	High
Medium	Medium	Medium
Medium	Low	Medium
Low	High	Medium
Low	Medium	Medium
Low	Low	Low

Appendix III. Information Requirements for conducting a Risk Assessment of potential invasive species

Information requirements for conducting a qualitative risk assessment are listed in Appendix III of the Code on Introductions and Transfers (CCFAM 2003). Section titles from this list are provided below. Details of the information requirements for each section are given in the Code.

A) Executive Summary
B) Introduction
C) Life history information of the species to be introduced or transferred
D) Interaction with native species
E) Receiving environment and contiguous watershed
F) Monitoring
G) Precautions and management plan
H) Business data
I) References

Items C to E are relevant for evaluating the potential *controlling influence* of invasive species on key components of ecosystem structure and function.

Rarity: a Criterion of Ecological and Biologically Significant Species?

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Interpretation of "significance"

The definition of significance used in this discussion paper is derived from the report of the workshop on Ecologically and Biologically Significant Areas (Ecosystem Status Report 2004/006). Specifically, in order to identify a species as significant, it is required that the ecological consequences following perturbation to the species would be relatively greater than those following perturbation to most other species in the community. As a result, an Ecologically and Biologically Significant Species may require enhanced management relative to other species that are not designated as significant.

Definition of rarity and causal mechanisms

In this discussion paper, I have adopted the use of the macroecological concept of rarity, and not just the narrow definition of low abundance. A useful source for a definition of rarity is the system presented by Rabinowitz (1981), who suggested that rarity may take a number of different forms (Table 1). In this scheme species are classified using three criteria: geographic range (wide or narrow), habitat specificity (broad or restricted), and local abundance (somewhere large or everywhere small). Only one of the eight possible combinations (wide range, broad habitat specificity, and somewhere large local abundance) is classified as common. The other seven are considered to include some form of rarity. Gaston (1994) provides a detailed discussion of types of rarity.

Table 1

Geographic range	Wide		Narrow	
Habitat specificity	Broad	Restricted	Broad	Restricted
Local abundance (somewhere large)	Common	Predictable	Unlikely	Endemics
Local abundance (everywhere small)	Sparse		Non-existent	

A number of causes of rarity have been proposed. The proximal mechanisms reduce to three categories: ecological specialization, lack of dispersal, and historical contingency. Further investigation of these categories (e.g. chapters in Kunin and Gaston 1997) examine nonproximal mechanisms that may cause ecological specialization. Among the suggested mechanisms are: breeding systems that favour selfing, low reproductive investment, low amounts of genetic variation, low population densities, and chaotic population dynamics.

Rarity as a criterion: some considerations

It has been established that in most ecological communities that comprise more than a few species, most of the constituent species are rare. The species abundance distributions of most communities tend to follow some form of lognormal or logarithmic curve, with most of the individuals found in just a few species, and the majority of species represented in relatively low numbers. A large research literature on the topic suggests that this high proportion of rare species is not simply just an artefact of low sampling intensity, but often an inherent characteristic of community structure. This "commonality of rarity" forces several considerations. One cannot simply declare any rare species as significant, as this will result in the designation of the majority of species in the ecosystem.

As a first consideration, it is necessary to revisit the definition (types) of rarity, and determine if any, or all forms of rarity are of relevance for identification of Ecologically and Biologically Significant species. Arguments can be made for most categories, but a state of low abundance (everywhere small) appears to be key characteristic, especially tied to a restricted range.

A determination of the appropriate spatial and temporal scale for evaluation of the ecological and biological significance of a rare species is necessary. For marine species, the spatial scale of relevance is likely the

ocean zone (Pacific, Arctic, Atlantic), or perhaps on a finer scale, the current DFO Regions. Guidance on appropriate spatial scale can also be drawn from COSEWIC's policy and practice concerning Designatable Units. In any case, there appears to be little value in designating a locally-rare species as significant if the species is locally abundant in other areas within Canadian waters.

Identification of an appropriate time scale is likely less of an issue in evaluating rarity than selecting a spatial scale. Again, there appears to be little utility in choosing a short time scale of order months to years. It may be useful to follow the approach provided in the framework for identification of Ecologically and Biologically Significant Areas (Ecosystem Status Report 2004/006). In this report it was suggested that the influence of longer term temporal variation should be addressed through periodic reviews and new evaluations.

One important issue concerning rare species is that often little is known about them. This makes evaluation of the ecological roles and significance of rare species difficult. However, rare species may be considered Significant for reasons other than rarity *per se*. For instance, rare species can be useful in monitoring changes to biodiversity. One reason is that since small populations are more likely to suffer extinction, rare species should be more sensitive to disturbance, and therefore useful for bioassessment (e.g. Diamond and May 1976; Gilpin and Soulé 1986). Also, there are examples in the literature of rare species that fill import roles in community structure and dynamics. An interesting example in the terrestrial literature is the case of native and exotic thistles in Nebraska, reported by Louda and Rand (2003) (in Kareiva and Levin 2003: The importance of species).

Thistles (*Cirsium* spp.) described in the above study are numerically minor species that provide an ecologically and economically valuable service: resistance to an invasive weed. Native thistles support insect populations that inhibit growth and spread of native thistles. However, these insects also target exotic (invasive) thistles that have spread into the study area. These exotic thistles have spread widely in other areas, but not in areas where the native thistle species are present. The authors have concluded that loss of the rare native thistle and its reservoir of native, specialized insects would be expected to increase the probability of a full-blown invasion by invasive thistle species, as has occurred in other areas. Thus the loss of native thistle and its insects could create an important weed out of a currently innocuous exotic plant. This case study suggests that ecological function and (potential) economic value of a species may not be obvious, and it cannot be assumed that rare (and even "obnoxious") species do not play a valuable or important role in community structure and function.

Tentative conclusion

Rarity in and of itself may not be sufficient to serve as a stand-alone criterion for identification of an Ecologically and Biologically Significant Species, given that most species can be defined as relatively rare. However rarity may be an important consideration in the interpretation of other potential criteria. This is somewhat similar to the inclusion of "Resilience" and "Naturalness" as dimensions in the evaluation of Ecologically and Biologically Significant Areas. In that Workshop report it is stated that these "two additional dimensions" are to be "considered when evaluating sites on the three major dimensions" (Ecosystem Status Report 2004/006).

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Ecologically Significant Species (EBSS)
Draft criteria for identification of significant toxic or harmful phytoplankton species

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Abstract

The general term *harmful algae* includes any phytoplankton species that is harmful to marine organisms, humans, other animals or the environment, including *toxic phytoplankton*, which produce *phycotoxins* that have observable toxic effects, and other *non-toxic* species which detrimentally affect other organisms by physical or chemical means. Harmful algal blooms (HABs) are a global phenomenon whose frequency and severity may be increasing worldwide. In Canadian waters, least 36 phytoplankton species are known to pose toxic or other hazards, including such phenomena as Paralytic Shellfish Poisoning (PSP), Amnesic Shellfish Poisoning (ASP; domoic acid), Diarrhetic Shellfish Poisoning (DSP), Spirolides, Yessotoxins, and Pectenotoxins, as well as ichthyotoxic and other phenomena which cause fish mortalities. This Working Paper establishes three criteria which are judged to be of primary importance in determining the potential significance of HAB species: 1) Ecological Effect, 2) Geographic Distribution, and 3) Frequency of Occurrence. The Effects and Distribution or each species are ranked as Limited, Moderate or Severe (Widespread), and the Frequency is ranked as Annual, Occasional or Rare. An evaluation table shows how these rankings apply to the known HAB species in Canadian waters, with information on the regions typically affected (as of 2006). The economic effects of HABs are not explicitly considered, but are recognized to be an important consequence of the ecological effects of these species. Other considerations which are important in a management context include the effect of anthropogenic environmental forcing (eutrophication, altered hydrological regime, climate change, dredging) and human-mediated species introductions (including ballast water transfer), which can affect the distribution and dynamics of HAB events. It is also noted that this document reflects the current state of knowledge at the time of publication and cannot anticipate future ecosystem changes. The practical application of these criteria in specific management situations will rely heavily on the existence of reliable, long-term monitoring data for HAB species. Presently, such data are incomplete or absent in many regions of Canada.

Definitions

The general term *harmful algae* includes any phytoplankton species that is harmful to marine organisms, humans, other animals or the environment. This term includes, but is not limited to, the *toxic phytoplankton*, which produce *phycotoxins* that have observable toxic effects. Other *non-toxic* species may be considered harmful if they detrimentally affect other organisms by physical or chemical means. The occurrence in the environment of these various toxic and harmful species is grouped under the general term *harmful algal blooms (HABs)*.

Introduction

Toxic or otherwise harmful species of phytoplankton are a global phenomenon that has received increasing attention and concern in recent years. There is a widespread perception that outbreaks (blooms) of toxic species are increasing in frequency and severity worldwide (Anderson et al. 2002, Hallegraeff 2003). This trend is generally acknowledged to be partially real and partially due to increased surveillance and reporting, prompted by economic and public health concerns associated with the seafood industry, especially the aquaculture sector (Glibert et al. 2005a). Irrespective of whether the frequency or severity of such events is increasing or not, toxic or otherwise harmful algal blooms (collectively known as HABs) are a widespread phenomenon that influences the health and productivity of aquatic ecosystems and the human socio-economic systems that depend on them. Globally, there are approximately 200 species of phytoplankton that are recognized as toxic or otherwise harmful (Landsberg 2002).

In Canadian waters, recognition of HAB species dates to the 1940s, when the dinoflagellate *Alexandrium tamarense* (formerly known as *Gonyaulax tamarensis*) was identified as the causative organism in Paralytic Shellfish Poisoning (PSP) (Medcof et al. 1947, Needler 1949). Both aboriginal populations and European immigrants had nevertheless recognized the phenomenon of shellfish poisoning for centuries (Prakash et al. 1971). In the latter half of the twentieth century, public health concerns prompted a considerable research effort and the establishment of routine shellfish monitoring programs to protect consumers and the seafood industry. Over the years, other poisoning phenomena have been recognized and new toxic phytoplankton species have been identified. Aside from PSP toxins, Canadians must contend with Amnesic Shellfish Poisoning toxins (ASP; domoic acid), Diarrhetic Shellfish Poisoning toxins (DSP), Spirolides, Yessotoxins, and Pectenotoxins (Bates & Forbes in prep., Bates 1997). In addition, some species are toxic but do not appear to affect humans, although their toxicity to other marine species may be very broad. The raphidophyte *Heterosigma akashiwo* is one such example (Table 1) (Black et al. 1991, Whyte et al. 1997). Added to this are non-toxic species that are nevertheless considered harmful by virtue of their noxious effects when they occur at sufficient population densities, including blooms of the diatom *Chaetoceros* spp., or the ciliate *Mesodinium rubrum*, both of which can cause fish mortalities (Martin et al. 2001). Currently, at least 39 species are known to pose a toxicity hazard or to have otherwise harmful effects in Canadian waters (Table 2).

Table 1: Species affected by the toxicity of *Heterosigma akashiwo* (compiled by E. Black).

Bacteria	**Rotifers**	**Fish**
- Undefined sp.	- *Brachionus plicatilis*	- *Oncorhynchus nerka*
Fungus	**Copepods**	- *Oncorhyncus tshawytscha*
- *Aspergillus niger*	- *Pseudodiaptomus marinus*	- *Oncorhyncus kisutch*
Algae	- *Arcatia omorii*	- *Salmo salar*
- *Skeletonema costatum*	- *Acartia hudsonica*	- *Oncorhyncus mykiss*
- *Chaetoceros* sp.	- *Acartia tonsa*	- *Seriola quinqueradiata*
- *Thalassiosira* sp.	**Crustacea**	- *Centropristis striata*
Tintinids	- *Artemia salina*	- *Cantharus cantharus*
- *Tintinnopsis tubulosoides*	**Bivalves**	- *Pagrus major*
- *Favella* sp	- *Mytilus edulis*	- *Pocelus mexicana*
	- *Crassostrea gigas*	

It must also be recognized that harmful and toxic species do not always cause harm, if their concentrations are sufficiently low relative to other phytoplankton species . In addition, the same species may be toxic under some conditions and non-toxic under others (e.g. *Pseudo-nitzschia* spp.; Bates et al. 1998). Indeed, many harmful species can at times represent important components of the food web, and their mere presence is not necessarily a cause for concern. However, the risk of HABs and their attendant effects on the health and productivity of the ecosystem clearly merit attention and vigilance. This working paper aims to establish a mechanism to identify which HAB species are *significant*, in an ecological context.

Draft Criteria

Three main criteria were judged to be of primary importance in determining the potential significance of HAB species: Ecological Effect, Geographic Distribution, and Frequency of Occurrence. Table 2 shows how these draft criteria apply to the known HAB species in Canadian waters; it also includes information on the region(s) affected, the toxin(s) involved and the mechanism(s) of action for these toxins and HAB species. The goal is to provide a tool for evaluating the importance of harmful algae in particular situations when setting conservation or management objectives.

Ecological Effect

The level of risk posed to the ecosystem and food chain (including commercially exploited species) depends on a variety of factors, including the role of the organism in the ecosystem and the extent or propagation of the toxin through the food chain. A wide variety of phycotoxins (algal biotoxins) are produced by the different toxic phytoplankton species occurring in Canadian waters. Each has its own specific toxicity, mode of action

and physiological effects on other organisms (including invertebrates, fish, marine mammals, birds and humans) that ingest it or are exposed to it. Species such as *Alexandrium fundyense*, *Heterosigma akashiwo*, *Karenia mikimotoi* and *Mesodinium rubrum*, which can result in the mortality of a wide variety of other organisms, can be particularly detrimental to the ecosystem. In addition, both the per-cell toxicity and the suite of toxins produced can vary within a species, depending on genetics, the environment, and the physiological condition of the particular cells in question (Parkhill et al. 1999). Some toxins (e.g. spirolides), while known to produce a toxic effect in laboratory mouse tests (usually by intraperitoneal injection), have no clearly demonstrated effects when ingested orally (Richard et al. 2000). Although attention tends to focus on toxic species, certain non-toxic phytoplankton can be harmful to fish and other marine organisms when present in sufficient numbers (Black et al. 1991). Various diatoms of the genus *Chaetoceros*, among others, are known to cause gill irritation and respiratory failure in both wild and cultured fish (Horner et al. 1997). Detailed discussion of the ecophysiology and toxicology of HAB species is beyond the scope of this document, but clearly, when determining whether a toxic or otherwise harmful species is "significant", some evaluation should be made of its toxicity or harmfulness, and therefore the degree of risk it poses within the ecosystem.

Toxic or harmful species may also exert economic effects, depending on whether or not they can cause significant disruption to industry and other human activities. For example, closures of molluscan shellfish harvesting due to phycotoxins, or the mass mortality of farmed fish because of harmful phytoplankton, have a significant economic impact. Such events also can have a "trickle-down" or "halo" effect by negatively affecting the sale of other food products derived from the ocean, as well as economic activities (such as tourism) related to the primary industry. In the context of the present exercise to identify Ecologically Significant Species, a harmful or toxic species will not be considered ecologically significant if its *only* consequences are social or economic. However, the social and economic consequences for humans are frequently themselves consequences of ecosystem effects since the socio-economic importance of a species is related to its ecological situation. Thus in the case of many toxic and harmful species, ecological significance will also imply economic significance.

In Table 2, the ecological effects of each toxic or harmful phytoplankton species are ranked as Limited, Moderate or Severe. In some cases, the effects are postulated, but unknown.

Geographical Distribution

An important criterion is the tendency of blooms either to become widespread or to remain localized. Species such as the PSP-producing *Alexandrium* spp. are nearly ubiquitous and are known for their tendency to form very large blooms that can spread over wide areas (e.g. Anderson et al. 2005). In Canadian waters, toxic *Alexandrium* species bloom in the estuary and Gulf of St. Lawrence, the Bay of Fundy, the south shore of Nova Scotia, coastal Newfoundland, and many coastal areas of British Columbia, resulting in closures, sometimes annual, of molluscan shellfish harvesting. *Heterosigma akashiwo* is likewise broadly distributed in coastal waters of southern British Columbia. Domoic-acid-producing *Pseudo-nitzschia* species have less often caused harvesting closures, but these have occurred on both the Atlantic and Pacific coasts. Other species have remained relatively localized. Figures 1, 2 and 3 show the known distributions of the major phycotoxin phenomena in Canadian waters. Individual species distributions are not shown, but an approximate indication is given in Table 2 for each species, along with a ranking of Limited, Moderate or Widespread occurrence.

Frequency of Occurrence

The mere presence of a given toxic or harmful species is not in itself a good indicator of its potential significance in the ecosystem. Some measure of the frequency of harmful outbreaks is necessary. Depending on regional and local oceanographic conditions and the species in question, HABs may recur frequently (in some cases, annually), or sporadically. In Table 2, the Frequency index is divided into two main components, Presence/Bloom and Seasonality. The former is ranked as Annual, Occasional or Rare, with a score given for both species presence, and bloom frequency. For example, a given species may be present annually in small numbers, but rarely forms large blooms. The Seasonality index shows during what part of the year the bloom or harmful phenomenon typically manifests itself.

Other Considerations

Natural and anthropogenic forcing

The development of a toxic or harmful bloom is always dependent on the environmental conditions under which is grows. As with any phytoplankton population, factors such as nutrient concentrations and flux, light regimen, and water column stability (influenced by heat and fresh water input) will favour the growth of particular species over others. While these factors are, of course, naturally variable, they can also be anthropogenically influenced. For example, eutrophication has long been suggested as an important factor in the development of toxic blooms in coastal waters (Anderson et al. 2002, Glibert et al. 2005b). However, analyses of long-term datasets from North America and Europe indicate that there is no convincing evidence that HABs and red tides are linked to eutrophication processes except in isolated unique events (ICES/OSPAR Workshop on Time Series Data Relevant to Eutrophication Ecological Quality Objectives, Sept 10-14, 2006; in prep.). Altered hydrological regimes resulting from changing land-use patterns or hydroelectric development may affect the distribution and frequency of toxic species such as *Alexandrium tamarense*, which is known to be sensitive to freshwater inputs, for example in the St. Lawrence estuary (Weise et al. 2002, Gagnon et al. 2005). Dredging is another activity that may stimulate the growth of HAB species, by resuspending phytoplankton cysts from the sediments. Obviously, anthropogenic (and natural) climate change can affect many oceanographic variables and thus may exert an important influence on HABs in the future. For example, there is evidence that increasing temperatures may favour the development of HABs in some environments by increasing their growth rate (Peperzak 2005) or by allowing them to migrate into areas not previously conducive to growth.

Invasive species

Invasive toxic or harmful phytoplankton species have prompted increasing concern in recent decades. While many HAB species have likely been ubiquitous for millennia, there are demonstrated cases of recent species introduction. The ballast water of ships is cited as one of several likely vectors (Rigby et al. 1993, McMinn et al. 1997, Carver & Mallet 2003), along with the transfer of aquacultured products from one site to another (Scarratt et al. 1993), and transport via birds and the hulls of ships. While potential introduction of a toxic or harmful species to a new area is cause for concern, discussion of the mechanisms of species transport is beyond the scope of this document. It is noted that the ESS workshop included a more general discussion on invasive species, and the threat of toxic and harmful species introductions should be considered in that context.

Conclusions

The issue of harmful algal blooms is complex, owing to the many species- and location-specific variables that come into play. This document focuses on three main criteria (Effects, Geographic Distribution and Frequency) which should be considered when judging whether a HAB species is significant in a particular ecological context. These criteria are obviously not exhaustive, but are judged the most relevant and simple to apply.

Clearly, the list of species and their effects shown in Table 2 is provisional, in that it reflects the current state of knowledge and cannot anticipate future ecosystem changes. It was noted by several PWG members that the practical application of these criteria in specific management situations would rely heavily on the existence of reliable, long-term monitoring data for HAB species. Presently, such data are incomplete or absent in many DFO Regions, a situation that can only hamper decision-making.

Table 2: Major toxic and harmful species in Canadian waters: Compiled with information from White (1980), Taylor & Horner (1994), Martin et al. (1995, 1999, 2001, 2006, in press), McKenzie et al. (1996, 1998a, 1998b, 2003), Bates (1997), Blasco et al. 1998, Bérard-Therriault et al.1999, Couture et al. 2001, Levasseur et al. 2001, Landsberg (2002), Schwinghammer (2004), Bates & Strain (2006), and Bates & Forbes (in prep.). Note: table is incomplete.

Species	Ecological Effect	Geographic Distribution	Frequency of Occurrence		Toxin(s)	Mechanism (Marine or Human)
	Limited **M**oderate **S**evere	**L**imited **M**oderate **W**idespread (**Atl**antic/**Pac**ific)	Presence/Bloom **A**nnual **O**ccasional **R**are	Seasonality **Spr**ing, **Sum**mer, **F**all, **W**inter		
Diatoms						
Amphora coffeaeformis	Unknown	W (Atl)	A/R (?)	Spr, Sum	Domoic acid (?)	Neurotoxic
Chaetoceros concavicornis	L	W (Atl, Pac)	A/O	Spr, Sum, F, W	None	Gill irritant; caged fish
Chaetoceros convolutus	L	W (Atl, Pac)	A/O	Spr, Sum, F, W	None	Gill irritant; caged fish
Chaetoceros debilis	L	W (Atl)	A/A	Spr, Sum, F	None	Gill irritant; caged fish
Chaetoceros socialis	L	W (Atl,)	A/A	Spr, Sum, F	None	Gill irritant; caged fish
Corethron criophilum	L	M (Atl)	A/R	Sum, F	None	Gill irritant; caged fish
Ditylum brightwellii	L	W (Atl)	A/O	Sum, F	None	Gill irritant; caged fish
Eucampia zodiacus	L	W (Atl)	A/O	Spr, Sum, F	None	Gill irritant; caged fish
Leptocylindrus minimus	L	W (Atl)	A/A	Spr, Sum, F	None	Fish mortality
Pseudo-nitzschia australis	S	W (Pac)	A/O	Spr, Sum, F	Domoic acid	Neurotoxic
Pseudo-nitzschia delicatissima	L	M (Atl, Pac)	A/O	Spr, Sum, F, W	Domoic acid (?)	Neurotoxic
Pseudo-nitzschia fraudulenta	L	L (Atl)	O/R	Sum, F, W	Domoic acid (?)	Neurotoxic
Pseudo-nitzschia multiseries	M	W (Atl, Pac)	A/O	Sum, F, W	Domoic acid	Neurotoxic
Pseudo-nitzschia pseudodelicatissima	M	W (Atl, Pac)	A/O	Sum, F	Domoic acid	Neurotoxic
Pseudo-nitzschia seriata	M	W (Atl, Pac)	A/O	Spr, Sum	Domoic acid	Neurotoxic
Species	**Ecological Effect**	**Geographic Distribution**	**Frequency of Occurrence**		**Toxin(s)**	**Mechanism (Marine or Human)**

	Limited **M**oderate **S**evere	Limited **M**oderate **W**idespread (**At**lantic/**Pac**ific)	Presence/Bloo m**A**nnual **O**ccasional **R**are	Seasonality **Spr**ing, **Sum**mer, **F**all, **W**inter		
Dinoflagellates						
Akashiwo sanguinea (Gymnodinium splendens)	M	W (Atl)	A/O	Sum, F	Unknown	Ichthyotoxic; oysters
Alexandrium acatenella		(Pac)			Saxitoxins	Neurotoxic
Alexandrium catenella		(Pac)			Saxitoxins	Neurotoxic
Alexandrium fundyense	S	W (Atl)	A/A	Spr, Sum, F	Saxitoxins	Neurotoxic
Alexandrium hiranoi		(Pac)			Saxitoxins	Neurotoxic
Alexandrium ostenfeldii	L	W (Atl, Pac)	A/R	Spr, Sum	Saxitoxins, Spirolides	Neurotoxic
Alexandrium pseudogonyaulax	L	M (Atl, Pac)	A/R	Sum, F	Goniodomin A	Antifungal effect Liver & thymus
Alexandrium tamarense	S	W (Atl, Pac)	A/A	Sum	Saxitoxins	Neurotoxic
Cochlodinium polykrikoides	Unknown	M (Pac)	A/O		Unknown	Ichthyotoxic
Dinophysis acuminata	L	W (Atl)	A/O	Sum, F	Okadaic acid, DTX, Pectenotoxin	Gastrointestinal
Dinophysis norvegica	M	W (Atl)	A/O	Sum, F	Okadaic acid, DTX, Pectenotoxin	Gastrointestinal
Dinophysis rotundata	L	W (Atl)	A/R	Sum, F	DTX	Gastrointestinal
Karenia mikimotoi /Gyrodinium aureolum	S (L)	L (Atl)	A/O	Sum, F	Gymnodimine	Toxic; marine organisms
Prorocentrum lima	L	M (Atl)	A/O	Spr, Sum, F	Okadaic acid, DTX	Gastrointestinal
Prorocentrum mexicanum	L	L (Atl)	A/R	Spr, Sum	Okadaic acid, DTX	Gastrointestinal
Prorocentrum minimum	L	W (Atl)	A/O	Sum, F	prorocentrrin?	neurotoxic?
Species	**Ecological Effect**	**Geographic Distribution**	**Frequency of Occurrence**		**Toxin(s)**	**Mechanism (Marine or Human)**

	Limited **M**oderate **S**evere	**L**imited **M**oderate **W**idespread (**Atl**antic/**Pac**ific)	Presence/Bloo m**A**nnual **O**ccasional **R**are	Seasonality **Spr**ing, **Sum**mer, **F**all, **W**inter		
Dinoflagellates (cont.)						
Protoceratium reticulatum	L	M (Atl)	A/R	Spr, Sum	Yessotoxin	Neurotoxic; Cardiotoxic in mice
Cyanobacteria						
Anabaena flos-aquae	L to S	Freshwater	A/A	Sum, F	Aratoxin, Microcystin	Neurotoxic Ichthyotoxic
Aphanizomenon flos-aquae	L to S	Freshwater	A/A	Sum, F	Saxitoxin	Neurotoxic Ichthyotoxic
Microcystis spp.	M	M (Atl, Pac)	A/R	Sum, F	Microcystin	Possible carcinogen
Others						
Dictyocha speculum	L	W (Atl)	A/O	Spr, Sum, F	None	Hypoxia; caged fish
Heterosigma akashiwo	S	W (Pac)	A/O	Sum, F	Unknown	Ichthyotoxic
Mesodinium rubrum	M	W (Atl)	A/A	Spr, Sum, F	None	Hypoxia; caged fish
Phaeocystis spp.	L	M (Atl, Pac)	A/O	Spr, Sum	None	Nuisance and deleterious effects

Maps: Risk Areas of Harmful Algal Bloom Events, Based on Historical Monitoring Records

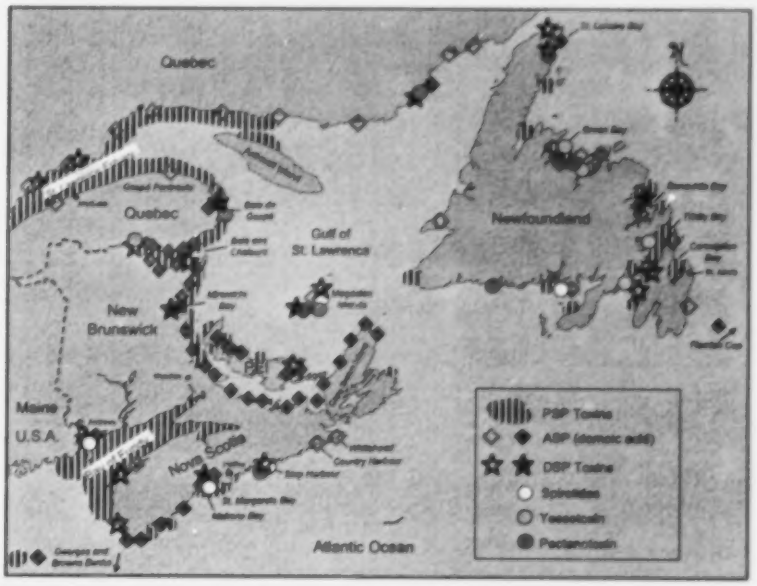


Figure 1. Harmful algal bloom risks in Atlantic Canada, as of 2005 (modified from Bates & Forbes, in prep.). Closed diamonds and stars represent closures of shellfish harvesting.

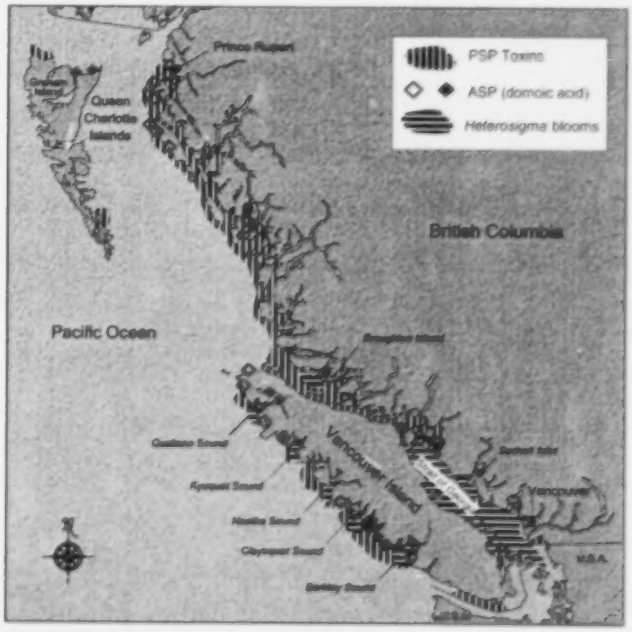


Figure 2. Harmful algal bloom risks in the Canadian Pacific, as of 2006 (modified from Bates & Forbes, in prep.). Closed diamonds represent closures of shellfish harvesting.

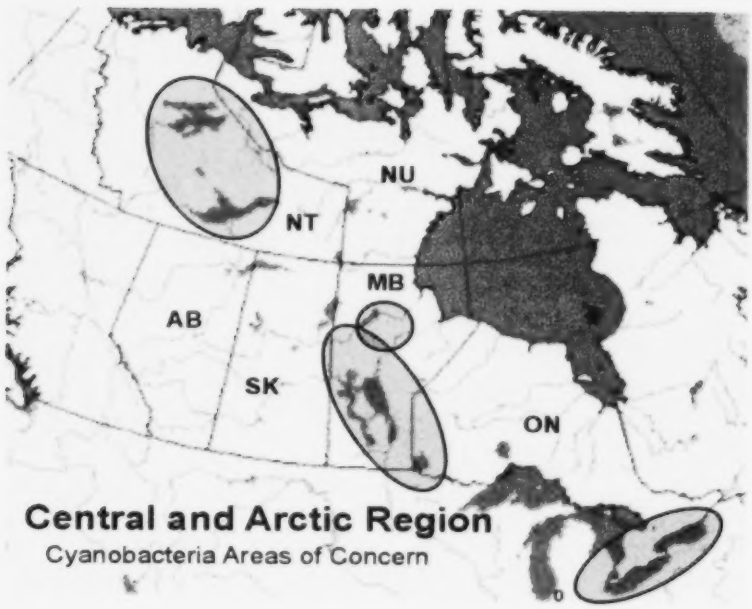
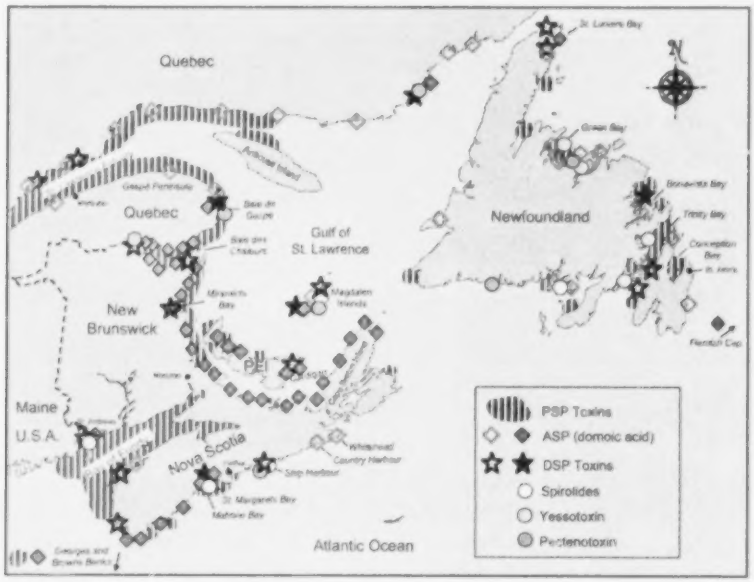


Figure 3. Harmful algal bloom risks in the Central and Arctic Region, 2005.

Maps: Risk Areas of Harmful Algal Bloom Events, Based on Historical Monitoring Records



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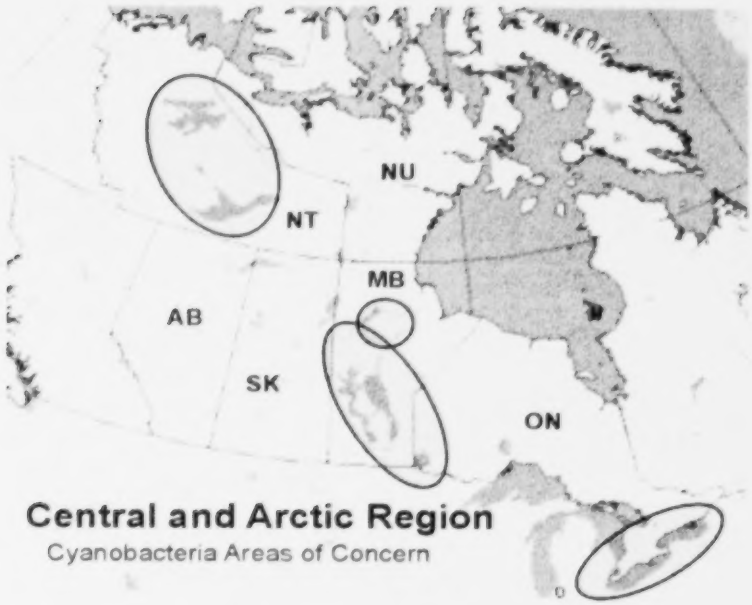

Figure 3. Harmful algal bloom risks in the Central and Arctic Region, 2005.

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Ecologically and Biologically Significant Species – Energy or Nutrient Importers/Exporters:

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Abstract

Keystone species are animals which through their activities and abundances regulate the productivity, diversity or physical structure of ecosystems or communities. Energy or nutrient importers/exporters are a class of keystone species that have received considerable attention in both freshwater and marine ecosystems. The Pacific salmon complex (*Oncorhynchus* spp.) provides especially well studied examples of the potential importance of highly influential energy and nutrient importing/exporting species associated with marine, freshwater and riparian ecosystems. Review of work conducted throughout the north Pacific rim supports the following conclusions. (1) Salmon serve as a limiting food resource for a diverse assemblage of predators, scavengers and decomposers such that salmon play a pivotal role in the maintenance of regional biodiversity in freshwater, riparian and to a lesser extent marine ecosystems. (2) Variations in salmon escapement and carcass deposition have a long term impact on variations in phosphorous (P) and nitrogen (N) delivery through re-mineralization processes that influence subsequent variations in the productivity of freshwater and riparian ecosystems that are often nutrient poor. (3) Maintenance of habitat and ecosystem integrity involves a positive feedback loop in which habitat structure and ecological processes are dependent on multiple influences of the salmon themselves. (4) Increases in salmon abundance reinforce biological linkages among marine, freshwater and riparian ecosystems while decreases weaken such linkages. (5) Disruption of nutrient delivery to aquatic ecosystems due to commercial harvest of salmon involves a range of consequences that may vary in severity from area to area depending on a host of interacting factors. Identification of sustainable salmon harvest levels has historically been considered as a relatively simple exercise focused on removal of adult fish surplus to requirements for "seeding" the next generation of returns. More recently sustainable harvest has become the focus for debates about tradeoffs between the immediate socioeconomic benefits of harvest versus the long-term, ecological benefits of reducing harvest to maintain key elements of regional biodiversity, habitat productivity and ecosystem integrity. Harvest and management of keystone energy or nutrient importing/exporting species in aquatic ecosystems is likely to involve complexities analagous to those emerging in association with developing effective ecosystem based management approaches for Pacific salmon.

Introduction

Ecological theory holds that certain animals exert a disproportionate influence on the ecosystems in which they live. Paine (1969) introduced the term "keystone species" to describe animals that through their activities and abundances regulate the productivity, diversity or physical structure of their communities. Implicit in the concept is that keystone species are exceptional in their importance relative to the rest of the community (Mills et al. 1993), that they are unique in their functioning within the community and that their impacts are disproportionately large relative to their abundances (Power et al. 1996). Loss of a keystone species results in significant changes in the structure or organization of a given ecosystem, with adverse consequences for the survival of other native species or populations (Helfield and Naiman 2006). In aquatic ecosystems, several species of fish and invertebrates play keystone roles as nutrient importers/exporters that exert a disproportionate influence at multiple trophic levels on diverse constellations of species with which they interact (Willson and Halupka 1995, Willson et al. 1998). Although many species have been identified as nutrient importers/exporters having a significant influence on aquatic ecosystems, Pacific salmon have been a focal point for a large body of research on this topic and are considered here for their heuristic value.

Pacific Salmon as a Keystone Energy and Nutrient Importers/Exporters:

Pacific salmon are commonly regarded as a keystone species in coastal ecosystems because of their widespread distribution (Slaney et al. 1996) and importance as a limiting food resource for a diverse assemblage of vertebrate predators and scavengers. They also serve as important delivery agents for marine derived nutrients (MDN e.g. phosphorus and nitrogen) that commonly limit production at the base of food-webs in freshwater ecosystems throughout the North Pacific rim (Stockner and Shortreed 1985, Gresh et al. 2000, Hyatt et al. 2004). Spatial and temporal variations in the abundance of spawning salmon can have

major effects on the dynamics of wildlife populations and on maintenance of regional biodiversity (Willson and Halupka 1995). For example, Cedarholm et al. (2000) documented over 137 species of vertebrates in addition to many invertebrates which use salmon as a food source. Ecological interactions between salmon and large carnivores such as bears demonstrate just how critical these interactions with wildlife may be. Studies of Alaskan, coastal brown bears suggest that almost all of their carbon and nitrogen is obtained from salmon and that a correlation exists between the autumn mass of female bears and their reproductive success (Hilderbrand et al. 1996). Indeed, the generally greater abundance of salmon appears to be the main reason for the maintenance of much higher densities of carnivores and scavengers in coastal as opposed to interior ecosystems (e.g. bears are 6-80 times more abundant on the coast, Miller et al 1997; see also Reimchen 2000).

The impact of large numbers of salmon returning to spawn in coastal ecosystems is not limited to just their direct consumption by carnivores and scavengers. Stable isotope analyses of sediment cores from Alaskan lakes (e.g. Finney et al. 2000, Gregory-Eaves et al. 2003) have provided results to suggest that variations in salmon escapement and carcass deposition have a long term impact on variations in phosphorous (P) and nitrogen (N) delivery that influence subsequent variations in the productivity of aquatic ecosystems that are nutrient poor. Stable isotope analyses of plant communities adjacent to spawning streams suggest that riparian plants may derive as much as 18-60 % of their foliar N from MDN imported from the high seas by spawning salmon (reviewed in Nelitz et al. 2006). Accordingly, variations of salmon returns in both space and time not only influence aquatic ecosystems but also have significant effects on the structure, growth and productivity of riparian vegetation (Naiman and Latterell 2005).

Naiman and Latterell (2005) provided an initial synthesis of how interactions between carnivores/scavengers and salmon may affect the cycling of MDN to shape not only freshwater and riparian ecosystems but also the long term viability of the contributing salmon populations. Adapting their work here (Figure 1), bears and other piscivores consume Pacific salmon, spreading salmon-enriched wastes and partially-eaten carcasses into freshwater and riparian-zone habitats (Helfield and Naiman 2006). Terrestrial and aquatic insects, colonizing the carcasses, enhance decomposition and diffusion of MDN. In the riparian forest, MDN are first re-mineralized by bacteria and then taken up by vegetation, increasing foliar N content and growth rates. Large riparian trees provide bank stabilization, shade, inputs of organic matter and large woody debris (LWD) thus improving the quality of in-stream habitat for salmon. LWD retains post-spawn, salmon carcasses in streams, further enhancing MDN availability. Increased foliar N content enhances palatability and nutrition of riparian plants, potentially altering patterns of browsing by wildlife. This may affect patterns of riparian plant productivity and species composition. The net result is a positive feedback loop that enhances the strength of ecosystem linkages, ecosystem-scale productivity and biodiversity (Fig. 1A) as long as keystone interactions between bears and salmon remain functional. By contrast, external events that result in major reductions of salmon and/or bears (e.g. climate induced mortality or harvest of one or both) have the potential to disrupt many of these processes thus potentially weakening ecosystem linkages (Fig. 1B) and ultimately the feedback effects these have on both salmon and bears.

Variations in the Importance of Salmon as Nutrient Importers/Exporters:

Although salmon may act as important agents for import/export of organic biomass and inorganic nutrients (e.g. phosphorus, nitrogen and trace minerals) that control production at the top and the base of food webs respectively, this role is unlikely to be of uniform importance in either space or time. For example, biomass and nutrient delivery or export functions of salmon in pelagic environments of the continental shelf or high seas are certain to be less important than in estuarine or freshwater ecosystems because salmon are widely scattered in the open ocean and represent only a small fraction of the biomass or production of all fish found there (Hyatt et al. 2006). By contrast, seasonal aggregations of both juvenile and especially adult salmon in estuaries and freshwater provide large pulses of both consumable biomass and inorganic nutrients against background conditions where one or both are often relatively scarce for much of the year (references in Cedarholm et al. 2000 and Stockner 2003).

Although inorganic nutrients (especially N and P) are known to commonly limit primary production of algal communities in coastal streams, rivers and lakes (Stockner and Shortreed 1985, Hyatt and Stockner 1985 and Hyatt et al. 2004), examination of regional distributions of total dissolved solids in aquatic habitats

suggests the distribution of nutrients is not uniform across large geographic regions even in freshwater (Fig. 2). Thus, nutrient dependent ecosystems may aggregate into clusters that exhibit varying levels of nutrient concentrations supporting a range of inherent productivity differences at sub-regional scale. For example, watersheds clustered in the area of Pitt, Banks and Princess Royal Islands along the eastern rim of the North Pacific in British Columbia's north coast appear to be especially nutrient poor (Fig. 2) while those clustered in the headwaters of the Dean, Bella Coola, Nimpkish (N. Vancouver Island) and Yakoun (QCI) rivers of British Columbia appear somewhat less nutrient impoverished. These patterns may be explained in terms of differences in regional bedrock geology which in combination with the erosive forces of weathering influence annual to seasonal patterns of inorganic nutrient and mineral loading within various watersheds. Thus, the watersheds exhibiting higher TDS values noted above are underlain by mixtures of sedimentary and volcanic rock which provide higher inorganic nutrient concentrations than those present in other coastal watersheds (e.g. Princess Royal, Pitt and Banks) dominated by nutrient poor, granitic rock and crystalline gneiss (Farley 1979, p.29). These differences alone help explain, in part, why long term production of all salmon originating from the Pitt, Banks and Princess Royale Island watersheds is lower than the aggregate production observed in other areas of similar size (Hyatt et al. 2006). These observations are clearly relevant to DFO's international (e.g. 1992 United Nations Convention on Biodiversity) and domestic responsibilities for maintenance of regional biodiversity (e.g. in Feb 2006 the government of British Columbia designated selected watersheds in and around Princess Royal Island as the Kitasoo Spirit Bear Protected Area for conservation of culturally significant Kermode bears, Russell 1994, McAllister et al. 1997). They are also significant to development of ecosystem-based management principles for implementation under DFO's new Wild Salmon Policy (Anonymous 2005.) because they indicate that disruption of nutrient delivery to aquatic ecosystems due to commercial harvest of salmon will involve a range of consequences that may vary in severity from area to area depending on a host of interacting factors (see also Nelitz et al. 2006).

Management Implications of Salmon as Influential Nutrient Importers/Exporters:

Pacific salmon are at once the subjects of one of the most advanced as well as one of the most cumbersome systems of fisheries management anywhere on the globe. Scores of fisheries harvest salmon from hundreds to thousands of populations and have done so for anywhere from a century (contemporary fisheries) to thousands of years (aboriginal fisheries). In spite of this enviable record of success, there are signs that significant changes are required in current day management practices in order to ensure the long-term sustainability of both salmon and salmon-dependent ecosystems. One of the major objectives of Fisheries and Oceans Canada's new Wild Salmon Policy (WSP, Anonymous 2005) is "to maintain habitat and ecosystem integrity" (WSP, Objective 2) because the health and well-being of wild salmon is inextricably linked to the availability of a diversity of interconnected and productive freshwater and marine habitats used by the Pacific salmon species complex. A growing body of credible scientific evidence suggests that maintenance of habitat and ecosystem integrity involves a positive feedback loop in which habitat structure and ecological processes are dependent on multiple influences of the salmon themselves (Figure 1). Consequently, salmon harvest levels, once considered to be a relatively simple exercise involving the removal of adult fish that were surplus to requirements for "seeding" the next generation of returns (e.g. Ricker 1954), have become the focus for debates about tradeoffs between the immediate socioeconomic benefits of harvest versus the longer term ecological benefits of foregoing harvest to maintain key elements of regional biodiversity, habitat productivity and ecosystem integrity (Grech et al. 2000). Thus, Reimchen (pp.93-96 in Harvey and MacDuffee 2002) has argued that average exploitation rates on salmon are 3-20 times those observed in most natural, multi-predator species communities and suggests that a long term, sustainable harvest rate should not exceed 5% for individual salmon populations!

Although statements such as Reimchen's may seem unnecessarily Draconian, they underscore the fact that salmon management has entered a period of increasingly complex and, oftentimes, competing objectives that are unlikely to be satisfied by traditional single species yield or assessment frameworks (Hyatt and Riddell 2000; see also pp. 72-79 of Cedarholm et al. 2000). Similarly, spatial and temporal interactions that depend not only on the state of salmon habitat but also on the influence that salmon may exert on the long-term productive capacity of these habitats suggests that the common practice of conducting salmon stock or salmon habitat assessments rather than assessments of the salmon stock-habitat complex will be increasingly inadequate as a basis for sustainable management of Pacific salmon in the future. Reflecting on what this implies about future assessment frameworks to improve management, Cedarholm et al (2000)

concluded that managing salmon as keystone species within an ecosystem context will require material, energy and nutrient budget analyses on appropriate spatial (e.g. PNCIMA, major river basin, sub-basin, stream) and temporal scales (months to millennia) to estimate the effects that land and fisheries resource management practices (past, present, future) have on ecosystems and salmon populations and that the latter have on ecosystems. Questions posed as relevant to the pursuit of this objective include:(1) What is the status of the nutrient capital and rates of transport within the various domains of salmon (nutrient budget)? (2) What is the range of the nutrient and materials capital and rates of transport (how does the current budget relate to the known range of standing stocks, rates of metabolism and transport for salmon)? (3) How have humans altered the nutrient budget? (4) What adaptive management actions might be warranted and feasible to push terrestrial and aquatic systems toward desirable goals? (5) What are the desired future conditions?

The WSP explicitly recognizes the folly of treating salmon and their habitats or ecosystems as separate entities for assessment and management. However, it also acknowledges a limited ability to immediately incorporate a wide range of ecosystem values and principles into salmon management given the complexity of the types of questions posed above and the Department's limited experience in designing, implementing and supporting ecosystem-based management* (EBM) frameworks. Regardless, it is obvious that the breadth and complexity of issues that must be engaged to ensure prudent management for the long term sustainability of the salmon stock-and-habitat complex recommends much greater efforts on this front.

*Ecosystem-based management has been defined as "an adaptive approach to managing human activities that seeks to ensure the coexistence of healthy, fully functioning ecosystems and human communities. The intent is to maintain those spatial and temporal characteristics of ecosystems such that component species and ecological processes can be sustained, and human well-being supported and improved." (excerpted from Anonymous 2004. The CCLCRMP Framework Agreement/Draft Interim Plan, Coast Information Team Document called Ecosystem-based Management Framework, April 2004).

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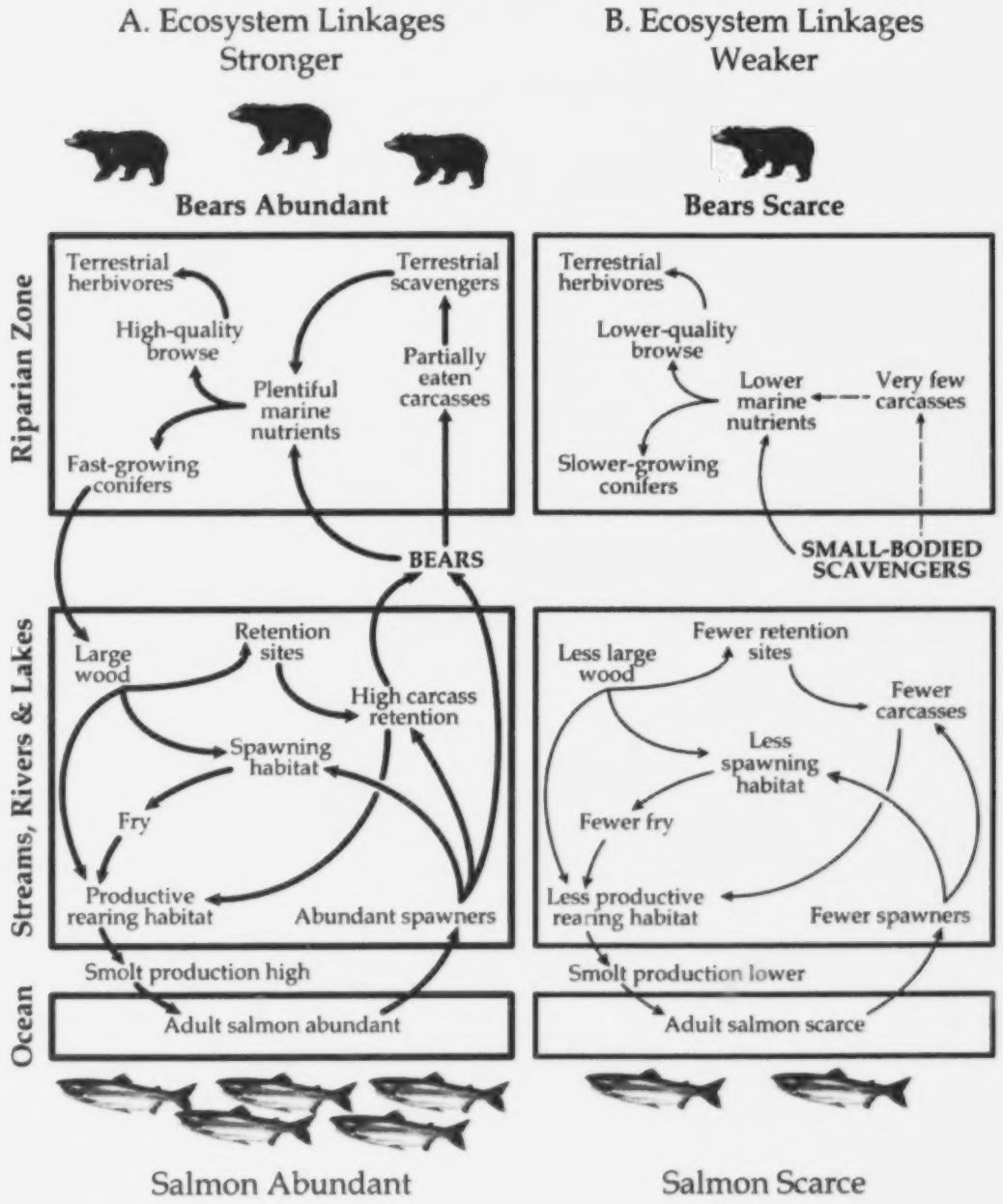

Figure 1. Conceptual summary of interactions among salmon and bears, acting as keystone species, in freshwater and riparian ecosystems. A. Ecosystem linkages are strengthened when both salmon and bears are abundant and B. Ecosystem linkages are weakened or eliminated if either bears or especially salmon become scarce. See text for details (figure modified here from Naiman and Latterell 2005).

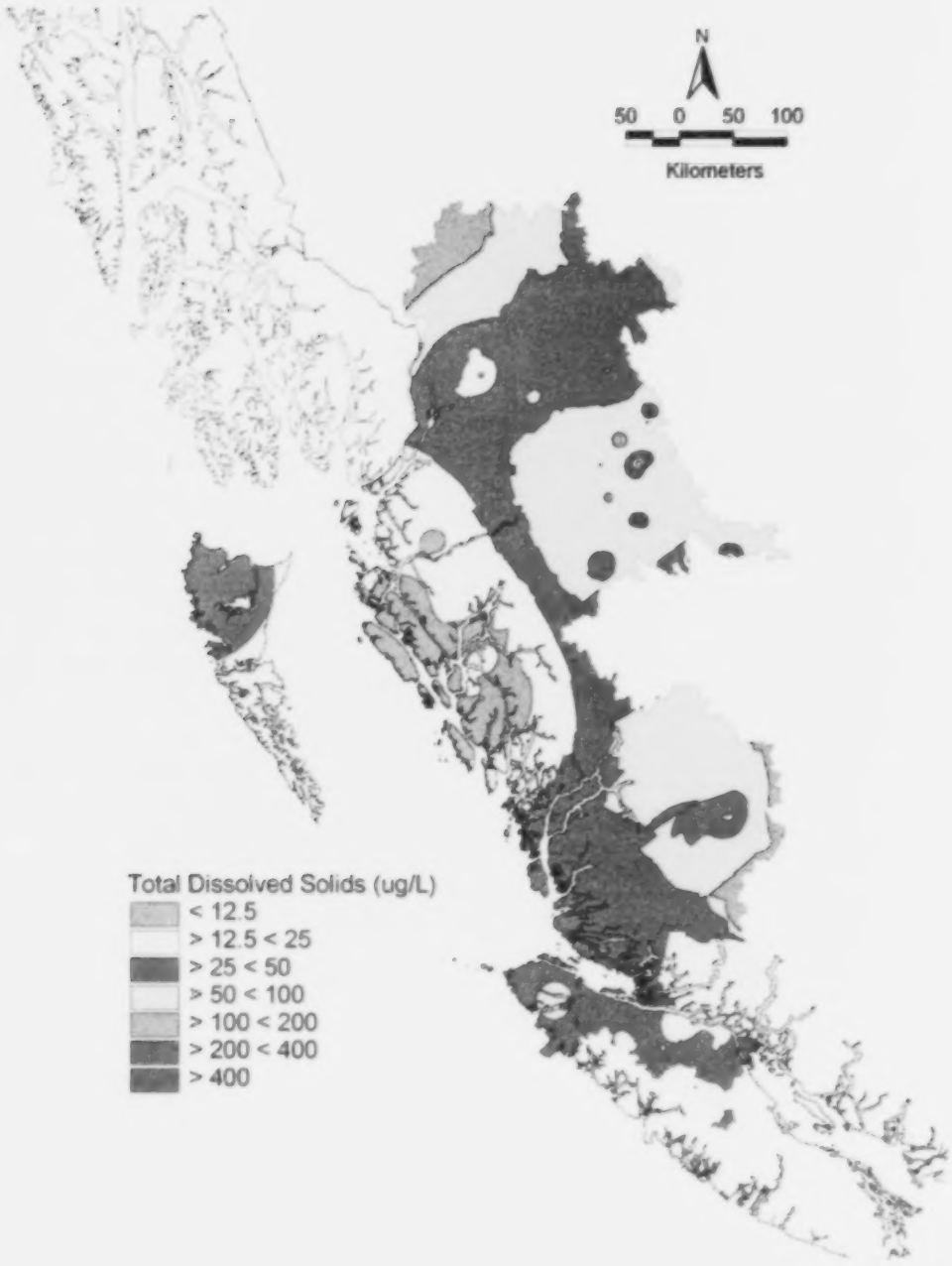

Figure 2. A summary of spatial patterns of total dissolved solids (TDS) present in freshwater rivers and streams sampled in hundreds of locations throughout the PNCIMA portion of British Columbia. Note unequal classification intervals from low to high end of scale. TDS observations from BC Ministry of Environment. TDS and figure format developed by Hyatt et al (2006).

Identification of Ecologically Significant Species: should iconic status and cultural importance be considered as criteria?

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Abstract:

This working paper presents background information and rationale to support the inclusion of iconic and culturally important species within the Ecologically Significant Species Framework currently being developed. Iconic species are defined as those animals that are no longer viewed by a significant segment of the world's population as natural resources to be used or, in some cases, even managed in a risk-averse way. Culturally important species are defined as species that through their capture, processing, distributing, celebrating and consuming define and promote a way of life as well as signify individual, communal, cultural and/or national identity. For many iconic species in Canada, particularly marine mammals, management and conservation initiatives are often influenced by the agenda's and policies of other national or international stakeholders (e.g. governments, conservation organizations and other NGOs). This can have a significant ripple affect throughout the Department in terms of strategic research and policy planning, development of ocean management plans, conservation and protection activities, and funding allocations. In the case of culturally important species, access on a long-term basis to species that are deemed important from a food, social and ceremonial perspective represents one of the fundamental cornerstones of land claim initiatives in Canada. The need for basic science and scientific advice on these species is embedded in the Department's obligations under the land claim in question. Failure to address these obligations would have significant consequences including breech of agreement intent in most cases and possible legal ramifications in others. Therefore, it is evident that both iconic and culturally important species are going to require enhanced management initiatives in the future. If the Ecologically Significant Species Framework does not address these requirements, then it will be important for the Department to propose alternative ways of effectively dealing with these issues in the near future.

General Comments:

This working paper presents background information and rationale to support the inclusion of iconic and culturally important species within the Ecologically Significant Species Framework currently being developed. Several points of clarification and discussion need to be made up front and flagged for consideration by the Workshop. Although the commentary presented here often uses marine mammals as a 'case study' to address issues related to iconic and culturally species, much of the background information and rational are broad enough to encompass certain fish species such as salmon, cod or charr. It should also be kept in mind that a species may be both iconic and culturally important as well as fit under another species or community criteria. In addition, it is possible that the status of a species (critical vs. not critical relative to a particular criterion) could change relatively quickly with a significant shift in the marine ecosystem (e.g. the effects of climate change). Thus, any framework for developing criteria to identify critical species should have the flexibility and decision rules to accommodate species that cross-cut criteria and those that may be affected by large scale oceanographic changes. Another pertinent discussion point regarding the identification of iconic and culturally important species is whether this criterion is nested under the requirement that the species in question also be ecologically important as defined by the steering committee. The presentation here assumes that 'some level' of biological/ecological importance is not a prerequisite for a species to be considered iconic and/or culturally important. Finally, can or should, a species that is important economically for a particular region of the country be considered as a critical species falling under either an iconic or culturally important criteria? Alternatively, should 'economic importance' regionally or nationally be considered a separate criterion? The following discussion presents background and comments that pertain to some of these questions.

Iconic Species:

Definition: Iconic species are those animals that are no longer viewed by a significant segment of the world's population as natural resources to be used or, in some cases, even managed in a risk-averse manner. To do so, some argue, degrades humanity and seriously compromises its ability to conserve the natural world for future generations (Corkeron 2006; Kalland and Sejersen 2005).

There are of course, varying degrees of iconic status, but certainly the mid-to-large sized cetaceans represent the pinnacle of this phenomenon both historically and at the present time. This group of marine mammals serves as a good case study to generally, discuss and evaluate rationale for identifying iconic species as *critical* species as well as exploring the risks and consequences for the Department if issues related to iconic species are not addressed. A general understanding of why certain species are imbued with this status, how the status evolves, and how iconography generally influences scientific research, management and conservation is a good starting point.

In the case of large whales, 'awe and mystery' as preserved by significant segments of the world's human population through-out history was the initial key to elevating the species-group to icon status. Over time it was generally felt that whales were magical and majestic in there own rights; this process was fueled by decades of whaling that had, and was continuing to decimate whale populations until the late 1960s (Corkeron 2006). The early 1970s were pivotal in terms of elevating whales to international icon status for numerous reasons, but the most important being the Stockholm Conference on the Environment (which was the start of the anti-whaling movement), the increasing influence of the IWC in world wide management and conservation of whales and the introduction of the U.S. Marine Mammal Protection Act. High profile writers and activists were also shaping people's opinions around the world. One of the most important books was Peter Matthiessen's 1971 *Blue Meridian* where he visited a whaling station and made the observation that "nothing is wasted except the whale itself." (Corkeron 2006). The conservation of whales had become a global concern where land-locked countries that had never whaled commercially or for subsistence, conservation groups, and animal rights activists, all had a say in how whales were managed in international forums. Depending on the iconic status of the species in question, science was no longer the foundation for whale conservation; politics, ethical issues and economics could be as important or more so (Hoyt 1991).

Implications of these evolving developments for management and conservation of whales and some pinniped species by national government agencies over the last two decades have been significant (Kalland and Sejersen 2005). Three general whale/marine mammal management paradigms have emerged – 1) 'whales' should not be used or managed for any human need (most often linked with more extreme animal rights movement; Regan 1984); 2) 'whales' may be used for non- or low-consumptive purposes that does not involve the deliberate killing or critical harming of animals (e.g. mainstream conservation groups that support eco-tourism/whale watching; Barstow 1986), and 3) 'whales' are renewable resources and should be used sustainably if managed with appropriate scientific advice and regulations (supported by nations involved in commercial, scientific and subsistence hunting of marine mammals; e.g. Hoel 1990). In Canada, management and conservation initiatives on iconic cetacean species generally support the center paradigm while at the same time try to protect the rights of First Nations and Aboriginal people to subsistence hunt. Pinniped management and conservation is more consistent with the third paradigm in most regions of the country.

From a research perspective, evidence of these management/conservation paradigms include a relatively new research emphasis on cetacean by-catch/ fishing gear interactions and mitigation options; strandings; effects of underwater noise (oil and gas exploration and future military activity); mitigating ship strikes; developing and providing basic science for responsible whale watching regulations; and documenting and mitigating coastal habitat degradation. Although many aspects of this research have valid stand-alone scientific merit and should be conducted under existing mandates, some aspects are driven by priorities other than science. In the case of iconic whale species (and any other species of similar status), this scenario is likely to continue into the foreseeable future and require Departmental attention. The somewhat circular and complicating aspect of this issue is that a significant portion of the above mentioned research has been initiated under SARA to conserve and recover threatened or endangered species that often have high iconic status. It is important to note that some (but not all) non-SARA iconic species will benefit from SARA-related

research and enhanced management given the overlap in life history characteristics and habitat requirements. However, inadvertently adopting the approach that SARA initiatives will eventually address all or most iconic species concerns is not a valid approach to take regionally or nationally. In the case of those pinniped species with iconic status, sound stock assessment research and strong regional scientific advice over the last 20 years has allowed DFO (as well as other Departments) to either directly address or to mitigate the numerous issues raised by conservation groups and animal rights activists. It is unlikely that DFO will be in a position to curtail involvement in these research areas in the near future.

Whether iconic species and issues related to them are dealt within the framework of ecologically significant species or under another Science or Oceans initiative is a point of discussion that will depend on how this workshop fine tunes the definition of a 'ecologically significant'. Regardless of this out come, the following points may provide guidance and justification for designating iconic species as critical.

An iconic species may be deemed critical if:

1. the management and conservation of the species is strongly influenced by policies, agendas or requirements of national or international stakeholders such as foreign governments, conservation organizations and other NGO groups

2. the above mentioned stakeholder requirements have a significant ripple affect throughout the Department in terms of strategic research and policy planning, development of ocean management plans, conservation and protection operations and Departmental allocation of funding and human resources

3. the above mentioned stakeholder requirements have ramifications that could adversely affect the livelihood of Canadian's, particularly aboriginal groups, who benefit from the appropriate management and conservation of iconic species

Culturally Important Species

Culturally important species can be considered from at least two different perspectives. The most straightforward being those species that are important to Aboriginal and First Nations people for food (subsistence), social and ceremonial use. The other more complex category includes those that are considered culturally important because they influenced how communities and particular regions of the country developed culturally, socially and economically, but are not considered a 'subsistence' food source.

At the semantic level it has been pointed out that the term 'subsistence' is complex and can be used in several ways (Freeman 1993): a) self-sufficiency often with the requirement that subsistence products should not enter the market but be consumed locally to meet nutritional and cultural needs; or b) a minimal level existence which could imply the resource uses are 'poor' and if they are not, then they are not engaged in subsistence activities. Clearly in our discussion here, we do not want to get bogged down debating the definition of 'subsistence'. The following comments in this brief consider culturally important species to be those that are important to Aboriginal and First Nations people for food (subsistence), social and ceremonial use. However, the Workshop does need to consider how, from a science perspective, the Department will deal with species that are culturally important but not from a subsistence perspective. The issue is more complex if the species in question is also economically important.

Definition: Subsistence species are those that through their capture, processing, distributing, celebrating and consuming define and promote a way of life as well as signify individual, communal and cultural and/or national identity (Langdon 1986; Wenzel 1991; Condon *et al.* 1995).

Few things are as important as food in any culture. For Aboriginal and First Nations people, the hunting, eating and sharing of country food (i.e. food hunted/fished from the land) with family and community maintains a relationship between themselves and their environment as well as with each other (Brice-Bennett 1977; Nuttall 1991; Wenzel 1991, 1995; Condon *et al.* 1995). From a nutritional perspective, country foods are usually a healthier alternative to what is available in some northern communities. This is particularly the

case for marine mammal foods given their high levels of omega-3 fatty acids that offer protection from cardiovascular disease and antioxidants like selenium that offer protection against heavy metal contaminants (Borre 1991; Freeman *et al.* 1998). Thus country foods are appreciated and valued for their nutritional benefits and the fact that they are also cultural symbols that underpin and strengthen personal well-being, individual and collective identity, and a way of life (Kalland and Sejersen 2005). Because hunting activities, and the consumption of the products of such activities, are intimately connected to such key values and traditions - people believe it is of paramount importance that they be passed on to the next generation (Price-Bennett 1977; Kalland and Sejersen 2005). However, during the last few decades northern societies have undergone dramatic changes (e.g. western-style schooling, increased dependence on wage labor and changing food preferences) that have made young people feel less committed to old traditions (eg. Condon *et al.* 1995). This has a negative effect on the transfer of knowledge between generations and it is a problem that aboriginal communities are struggling to deal with. Thus, maintaining cultural ties to the land through subsistence hunting is seen as a priority for many Aboriginal and First Nations people. One of the ways this is being accomplished is through land claim settlements and the subsequent establishment of varying degrees and types of self government.

Access on a long-term basis to species that are deemed important from a food, social and ceremonial (FSC) perspective represents one of the fundamental cornerstones of land claim initiatives in Canada. Aboriginal and First Nations peoples have a right to hunt and fish any species at all times of the year throughout their claims area to the quantity needed for their FSC purposes. In cases where there is a conservation concern, domestic harvest levels are established to protect and conserve the resource in question. The domestic harvest level usually constitutes a first demand against any commercial total allowable catch for the species in question (e.g. the Labrador Inuit Land Claim Agreement). The policy and operational implications of these rights from a Departmental perspective vary from one region of the country to another, but they are extensive (particularly for the Central and Arctic and Pacific) and touch most Sectors and Branches. In a brief overview such as this, it is not possible to drill into the details of these implications. However, the important point to recognize for our discussions here is that exiting Land Claim agreements by their nature represent the framework that enables signing parties to move towards a co-operative approach for managing and conserving culturally important species (K. Andersen pers. comm.). For First Nations peoples and Métis who do not have Land Claims, the Department still addresses their FSC requirements with the same objective of co-operatively managing and conserving the species in question. The need for basic science and scientific advice on culturally important species is embedded in the Department's obligations and commitments under the land claim in question. Failure to comply with these obligations would have significant consequences including breech of agreement intent in most cases, and possible legal ramifications in others. Presently, the Department has a strong and evolving science role to play relative to the management and conservation of culturally important species. With the ratification of new land claims over the next decade this role is certainly not going to diminish.

Thus, in addition to the Department's various mandates related to land claims, the following points may provide further justification for designating subsistence species as critical. A species is deemed critical if its hunting or fishing promotes and maintains:

1. a strong relationship between people, their environment and their way-of-life
2. well being through recognition of individual and cultural and/or national identity
3. opportunities for people to achieve greater self-sufficiency
4. improved nutrition and general health of people

Summary Remarks

Some iconic and culturally important species will be candidates for enhanced management because they are either listed by SARA or they will fulfill the requirements of one of the other selection criteria being discussed in this workshop. However, it must be noted that iconic and culturally important species that do not fall into one of these two categories may still be 'critical' or 'significant' to the Department from several different mandate and obligation perspectives. If iconic status and cultural importance are not included as criteria in the Ecologically Significant Species Framework, then there must be a discussion on how to deal with 'significant' species that do not fall into the two categories mentioned above.

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Emergent Properties of Communities

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The decision to identify some species as significant and others as not, will always be an arbitrary anthropocentric decision. It may be based on the perceived role the species plays in the overall functioning of the ecosystem, the ecosystem services it provides to humans, its commercial value, or some other criterion. Each of these are human valuations that imply some desired outcome from a human perspective

Biodiversity, that is the species richness and composition of any given marine ecosystem, relates to both the productivity and stability of that ecosystem (NRC 1995, Hubbell 2001, Worm and Duffy 2003). Changes in biodiversity, manifested either as reduced species richness or changes in the proportional composition of the component species, can result in complex reorganizations of such ecosystems. Such reorganizations exhibit changes in production and stability and are mediated through changes in trophic interactions that can result in trophic cascades and shifts to undesirable states of the ecosystem. These reorganizations in turn have impacts on the richness and particular species composition of the reorganized ecosystem. Thus feedback mechanisms initiated by changes in biodiversity can cause further changes in biodiversity. The specific mechanisms responsible for such reorganizations of ecosystems are poorly understood. To fill in these gaps in knowledge and to foster ecosystem-based management of human activities in marine systems, it is essential that we increase our knowledge of the linkages of biodiversity (and changes to biodiversity) to changes in trophic interactions (productivity) and spatial and temporal stability. Without such knowledge, and given the relatively non-selective impacts of most human activities on biodiversity (e.g., fisheries bycatch of a broad array and high biomass of non-target species), it will be challenging to achieve one of the primary ecosystem-based fisheries management goals, namely minimizing the risk of irreversible change to natural assemblages of species and ecosystem processes.

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Size Based Properties of Ecosystems

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Body size is central to the structure and function of food webs (Elton 1927) because body size is a fundamental determinant of energy flow, species diversity, and population densities (Pimm 1982, Peters 1983, Peters and Wassenberg 1983, Elser et al. 1996). For at least two reasons changes in community size composition should be indicative of changes in energy flows and of basic community structure.

Many life-history functions have been shown to scale with body size (Charnov 1993, Charnov and Gillooly 2004). These functions include many of the processes traditionally forming key parts of single-species population dynamics models, such as growth rate, maturation schedules, fecundity, and natural mortality. Hence measures of size-based community properties may capture the aggregate dynamics of these processes for the community as an interacting unit. This is more than just a speculative hope, as some studies have found size-based models to perform well (and better than structurally more complex species based models) when fit to real-world data on community trends (Pope et al. 2005, Hall et al. 2005).

Size is also important at the ecosystem scale because it integrates trophodynamic relationships across predators and their prey. A number of studies, going back to Hardy (1927) have shown that marine fish feeding has an extremely strong size dependence in marine systems, such that the diet of, say 70 cod, haddock, whiting, and plaice are more similar (although not identical, of course) than the diets of 20 and 70 cm individuals of each of those species (Pope 1991, Rice et al 2001). It is this size dependence of predation that allows wasp-waist structured systems, for example, to adjust to booms and collapses of the nodal prey species through changes in productivity (and diets) of the component species, rather than experience wholesale species losses and replacements, and, in relatively short time periods re-establish an orderly size composition of the community (Rice 1995, Cury et al 2000, Shannon and Cury 2004)

Consequently there has been substantial interest in size-based ecosystem indicators that might change due to fishing and other factors, and some have been found to be explanatory of fishing induced changes at a more system-wide level, particularly the community size spectrum (CSS - The Community Size Spectrum is defined by the distribution of numbers by size interval across the sampled size range, and idealiy across the whole community). The original theory of size spectra (Sheldon et al.,1972, Borgman 1987, Boudreau et. al 1991) was developed for the entire ecosystem, from primary producers to the largest predators. However, survey data are never available for the full ecosystem, from less than mm to tens of meters, and even monitoring data covering the range from some tens of mm (zooplankton and fish larvae) to a couple of meters (large fish, elasmobranches and seals) involve sampling areas with multiple gears which are difficult or impossible to inter-calibrate.

Fortunately, a number of studies have show that the size spectrum for subsets of the community that can be surveyed in a consistent way over time do show lawful patterns, and vary lawfully with at least fishing pressure. Using time series of survey information these indicators have been estimated for a number of systems (Greenstreet and Hall 1996, Rice & Gislason 1996, Duplisea et al. 1997, Greenstreet et al. 1999, Bianchi et al. 2000, Zwanenburg 2000). Fishing or other factors may change the abundance of organisms of different size classes, particularly the numbers of larger animals which then affects the slope of the descending limb of the size spectrum. In an exploited community, larger fish (and other organisms) generally suffer higher mortality related to fishing than smaller individuals. This may cause the size distribution to become skewed toward the smaller end of the spectrum (Zwanenburg 2000), and lead to an increase in the slope of the size spectrum over time with increasing fishing pressure. Gislason and Rice (1996), Rice and Gislason (1996), and Zwanenburg 2000) showed that an increase in exploitation resulted in a decrease of the larger, exploited, size classes, but in an increase of the smaller size classes due to a reduction in predation pressure. Both the intercept and the slope of the CSS vary (quasi)linearly with fishing mortality rate (Rice and Gislason 1996; Benoit and Rochet 2004, Anderson and Beyer 2006). Given these properties the CSS may constitute and indicator of fishing or other size selective effects on the community under consideration.

The slope and intercept of the CSS are not the only size-based properties that may be informative of the size composition of a community. OSPAR (the Oslo-Paris Commission) and the North Sea Council of Ministers requested advice from ICES on a number of ecosystem indicators for implementation of Annex 3 of the Bergen Declaration on Environmental Quality of the North Sea. With several years of analytical testing, ICES concluded that a metric as simple ar the percent of "large" fish in consistent survey time series was a reliable and fairly sensitive indicator of human perturbation of marine fish communities. What size is "large" for a survey series depends on the inherent productivity of a particular system, and its history of exploitation prior to the onset of the time series, but can be identified readily for the cases examined (ICES 2005 and 2006 ACE advice – still in press).

Thus, size-based properties of a community are ecologically and biologically significant; they reflect important structural and functional properties of ecosystems that are hard to measure directly. There is a theoretical basis for interpreting their patterns, and particularly changes in their patterns over time. There are both empirical field and simulation studies documenting the theoretical framework, and linking the framework to specific human activities in marine systems. Finally, there are some indicators with well-investigated properties for case-specific application of size-based approaches to studying marine communities and the impacts of human activities on them.

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Cumulative Abundance Across Species in a Community

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The positive relationship between habitat complexity and community diversity has been a cornerstone of community ecology (MacArthur 1972, Cody and Diamond 1975, Morris 2003, Chase 2005), even though many details of system productivity, disturbance regime, etc affect how diverse a particular community may be, given the features of the habitat (Chesson 2000, Hebert et al. 2004, Jonzen et al 2004, Shepherd and Litvak 2004). It is also well documented that across habitat gradients the abundance of each of a community of species alters because of differences in both their intrinsic productivities and the degree to which they are adapted to the habitat characteristics along the gradient (Fretwell and Lucas 1969, Fretwell 1972, MacCall 1990, Langton et al. 1996)

These two processes combine to give any delineated area a characteristic frequency distribution of abundances across species, a property that has been of interest to ecologists for many decades (Elton 1927, Fisher et al 1943, Preston 1962) and a cornerstone of the theoretical basis for biodiversity science (Hill 1973, Huston 1994).

Researchers on coastal point-source pollution noted several decades ago that a common effect of pollutants was to change habitat quality in a particular way. Instead of supporting a relatively large number of species (for the given region) with a range of abundances from a few quite common species, through progressively less common species to a fair number of uncommon and rare species, a few species could tolerate the presence of the pollutant whereas most species in the community could not. As a result the few tolerant species became (at least comparatively, if not absolutely) very abundant whereas the large majority of species were either eliminated from the area or fell to very low abundances (Hart and Fuller 1979, Spellerberg 1991). These community-scale impacts of pollutants were captured readily in plots of the cumulative abundance in numbers across the species in the community (rank-ordered from commonest to rarest). More recently similar effects have been shown for particularly successful invasive species (Hayes et al. 2005, Munawar et al 2005, Strecker et al. 2005, many others), where again the the cumulative distribution of abundance across species can be profoundly changed.

There is a growing interest in the role of habitat in marine and freshwater community dynamics (cf, Journal of Fish Biology 2005, vol 67, Rice 2005). Although there is not yet full consensus among experts, there is substantial and growing evidence for the generalisations that any activities which reduce habitat complexity consistently can be seen in an increasing skewness in the cumulative frequency of abundances across species. Likewise there are conjectures that effects of habitat rehabilitation such as construction of artificial reefs (Powers et al 2003, Perkol-Finkel and Beniyahu 2005, others) can be captured as reduced skewness in the CFD of abundances.

This property is attractive as an ecologically and biologically significant property of a community because it may directly reflect both diversity and complexity of the community. The cumulative frequency of abundance across species can be readily assembled from tractable amounts of sampling, whereas it is very difficult to accurately estimate the richness of a community (Huston 1994, ICES 2005). There is good theory from the early years of community ecology for interpreting changes in frequency distribution of abundance across species in the context of ecosystem structure and function, without having to make (usually poorly documented) assumptions about the functional role of individual species in the ecosystem, or estimate abundances of individual species with accuracy and precision. The CFD has been documented to respond lawfully to pollution, eutrophication, and invasive species (ICES 2005). It reflects impacts of human activities on habitat quality, which is a major consideration in the Ocean Action Plan framework, but is also difficult to measure directly and montor regularly in all but nearshore areas.

Again, there is also a well-studied indicator that can be used for real-world applications. K-dominance curves, measure the dominance (in number or weight) of the k most dominant species (Lambshead et al. 1983), and "k" can be extended to the full set of species in a series of samples (ICES 2005). The k-dominance curves of disturbed communities will differ from those in unperturbed communities (Rice 2000,

Bianchi et al. 2000), and statistical tests exist for comparing curves over time, or from different areas (Clarke 1990). Consequently, changes in K-dominance curves can be indicators of significant changes in the milieu of the ecosystem in question.

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Benthic-Pelagic Coupling

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Coupling between pelagic and benthic ecosystems directly affects the biogeochemical cycling of elements in the oceans and the micro and macro ecology of marine ecosystems. It also determines the potential of the oceans to sequester material over millions of years. Benthic and pelagic systems are linked through myriad biological, physical, and geological processes that operate over multiple spatial (centimetres to thousands of kilometres) and temporal (minutes to decades) scales (Snelgrove & Jumars; http://www.geo-prose.com). For example, terrigenous organic carbon originating from river and groundwater discharge, coastal erosion, sea-ice input, and aeolian material fluxes play an important role in the benthic pelagic coupling (Rachold et al. 2004).

Here we focus on the biological processes important to benthic-pelagic coupling, but it is stressed that these occur against a complex background of physical, environmental and geological forces. Biologically, benthic-pelagic coupling can be summarised as the quantitative relationship between biological processes occurring in the pelagic layer and the benthos (Boon 1998), that is, the cycling of nutrients between the bottom sediments and overyling water column. Water column depth and primary production are two key factors controlling the rate and extent of food supply to deep-water communities.

Primary production in the overlying pelagic system is based primarily on microscopic unicellular algae (phytoplankton). Algae utilise light to produce organic matter by photosynthesis, thereby reducing CO_2 while releasing O_2 and producing carbohydrates, which according to the needs of the algae, can be converted into essential compounds such as proteins and nucleic acids by incorporating nitrogen, phosphorus, sulphur, and other elements. The produced organic matter is eaten by herbivorous grazers, mainly zooplankton, which in turn may be eaten by fish, ultimately ending in top carnivores, with a loss of 75-80% of the organic matter from one trophic level to the next (Sakshaug 2004). The main losses are associated with respiration within the organisms themselves, microbial degradation of dissolved organic matter, sinking cellular remains and fecal pellets, thereby releasing CO_2 and nutrients. Zooplankton contribute in different ways to pelagic-benthic coupling: Their faecal material is a major route of energy flow and the vertical migrations of many species as well as the production of pelagic larvae by benthic organisms represent different paths to link the two subsystems.

The spatial and temporal distribution of the organic matter originating from the pelagic system is highly affected by the physical and hydrodynamic variables such as ice cover, fronts, gyres, internal waves and tides, upwelling regions, input of freshwater, and vertical stratification. Thus, only a small fraction of the organic matter reaches the seabed in different areas (Sakshaug 2004). Part of the carbon reaching the ocean floor is buried in the sediment and, therefore, sequestered from the atmosphere for millions of years. Another generally much larger part of the carbon export is remineralised by the benthos into CO_2, dissolved organic carbon (DOC) and nutrients, which are re-mixed into the hydrosphere. Finally, a third pool of carbon is dynamically stored in the biomass of the benthos (Klages et al. 2004).

Knowledge of primary production, and the factors influencing its spatial and temporal succession, has advanced far enough to be able to explain some aspect of the benthic-pelagic coupling in different areas throughout the world including the Gulf of St. Lawrence (GSL) and the adjacent Scotian Shelf. Ambrose and Renaud (1995) concluded that for similar depths and substrate types, the benthic biomass in the Arctic appears to be greater than at lower latitudes; suggesting that a greater proportion of the primary productivity may be cycled through the benthos in the Arctic than in temperate or tropical regions. In the GSL, the CJGOFS program show (a) that the upper layer of the GSL can be adequately modeled by considering only the vertical processes and that vertical mixing of intermediate strength favours enhanced algal biomass, (b) that autotrophy dominates during winter and spring and heterotrophy during summer and fall, (c) that nitrate uptake can contribute significantly to the production of small rather than large phytoplankton cells, indicating a certain degree of uncoupling between new production and carbon export, (d) that mesozooplankton do not exert a strong grazing control on phytoplankton biomass, but contribute up to 50% of the sinking flux of particulate carbon from the upper layer principally in the form fecal pellets and small zooplankton organisms, (e) that POC fluxes observed at 50 m were roughly similar throughout the year, suggesting that increased

export of detritus and DOC takes place during winter and spring, (f) that roughly 10% of the carbon fixed by phytoplankton reaches the bottom sediments and only 4-5% actually gets buried, (g) that the organic matter supply affects the composition of the benthic macrofauna, and (h) that the inorganic carbon content of the sediments varies little with depth inside the sediment (see review in Roy et al. 2000). However, many questions remain unanswered concerning the relation between pelagic physical and biological processes and the structure and functioning of benthic ecosystems. In that context, the Ocean Research Interactive Observatory Networks (ORION) (Benthic-pelagic coupling working group) recently developed a new research project. The objectives of this project are: 1) determine the spatial and temporal coherence of benthic-pelagic coupling, 2) determine how the benthic ecosystem reflects the pelagic ecosystem, and the mechanisms by which the pelagic ecosystem structures the benthic ecosystem, and 3) assess the importance of episodic events and seasonal processes in structuring benthic-pelagic interactions (Snelgrove & Jumars; http://www.geo-prose.com).

Relative proportionality of benthic / pelagic / demersal species

In addition to benthic-pelagic coupling provided by direct carbon export from plankton to the benthos (death, faeces), other links are provided through species interactions. These may be through complex food webs, or simpler, more linear systems such as seen in the Baltic Sea or the Arctic that transfer energy between the pelagic zone and the benthos. In some cases species important to benthic-pelagic coupling have been identified, such as the role of small pelagic fish in the up-welling Benquela system (Cury et al. 2000). Small pelagics, as predators of zooplankton and prey of benthic fish transfer energy from the pelagic zone to the benthic zone. In this case, the system may be "wasp-waisted" where the forage fish can exert top-down control on zooplankton, or bottom-up control on their predators, depending on their abundance.

There are many factors that may influence bentho-pelagic coupling through species interactions, some of which include:

- The seasonal/pulse aspects of bentho-pelagic coupling
- Life history of the species – many species transition between pelagic and benthic modes during their life history (e.g., larval and juvenile fish as plankton feeders, adults as benthic feeders; meroplankton of benthic invertebrates), thus species may be more or less important for benthic-pelagic coupling at different life history stages.
- The role of the meio and macro benthos in detritus mineralization by bio-turbation and bio-irrigation
- The role of specific species, e.g., marine mammals, small pelagics, benthic filter feeders as a link between pelagic and benthic zones.
- Add to this list?

The relative importance of different species for benthic-pelagic coupling is difficult to assess, and we have little knowledge of the dynamics and specific role of the benthic species (macro and meiofauna and bacteria). Furthermore, other than for species of commercial interest we have few estimates of abundance. However, we can begin to assess the strength of flows and pathways between benthos and pelagic zones through the analysis of trophic relationships, food web structure and ecological modelling. Minimally, we can estimate the proportion of benthic:pelagic species in the ecosystem, at least for those species for which we have abundance estimates.

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Le Changement du Rapport du Nombre de Niveaux Trophiques Supérieurs et Inférieurs : Utile pour Identifier les Espèces D'Importance Biologique et Écologique (EIBE) ?

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Énonce du Probleme

Reformuler le problème

Sous sa forme initiale, l'énoncé de la question comporte un certain nombre de sous-entendus. Par exemple, il est question du rapport du nombre de niveaux trophiques de deux catégories (les niveaux inférieurs *versus* les niveaux supérieurs). Ceci sous-entend qu'il y aurait au moins deux classes homogènes de plus d'un niveau trophique chacune. Or ce postulat ne s'applique pas bien aux autotrophes.

La deuxième implication est qu'une espèce ne peut appartenir qu'à un seul niveau trophique : ceux-ci seraient organisés de façon linéaire. Or ce n'est pas le cas. Dans les systèmes aquatiques, beaucoup d'espèces de poissons sont « ontogomnivores » : les individus se nourrissent à différents niveaux trophiques selon l'étape ontogénique où ils se trouvent, y compris sur des espèces dont ils sont la proie en début de cycle vital (voir références dans Montoya et al., 2006). Les sous-entendus de la question ne tenant pas, j'ai donc reformulé le problème autrement. L'énoncé ne fait appel qu'à la longueur de la chaîne trophique : « Le changement de la longueur d'un réseau trophique peut-il être utilisé pour identifier les EIBE ? »

Des cas triviaux ?

En première analyse, certains cas peuvent sembler tenir de la trivialité. Le cas trivial le plus évident semble être celui d'une espèce unique occupant un niveau trophique donné. Contrairement à ce qu'on observe chez les prédateurs supérieurs, les niveaux trophiques inférieurs se caractérisent par la redondance, en particulier les détritivores (voir références dans Naeem and Li, 1997). Il arrive que la disparition d'une seule espèce de détritivore ait des effets majeurs sur le flux de carbone (Taylor et al., 2006), ce qui est beaucoup moins prévisible que chez les prédateurs de niveau supérieur.

Change in the Ratio of the Number of Higher and Lower Trophic Levels: Usefulness to Identify the Ecological and Biological Significant Species (EBSSs)

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Issue Statement

Reformulating the issue

The initial wording of the issue statement contains a certain number of hints. For example, it mentions the ratio of the number of trophic levels of two categories (lower levels *versus* higher levels). This implies that there would be at least two homogeneous classes of more than one trophic level in each one. In reality, this postulate does not adequately apply to autotrophs.

The second implication is that a species can only belong to one trophic level, which would be organized in a linear way, and which it is not the case. In aquatic systems, many fish species are "life-history omnivores": individuals feed on various trophic levels according to their current ontogenetic stage, including on species of which they are the prey at the beginning of their life cycle (see references in Montoya et al. 2006). These hints being wrong, I thus reformulated the issue differently. The statement only calls upon food chain length: "Could we use the change in the length of a food web to identify EBSSs?"

Trivial cases?

In the first analysis, certain cases may seem to be trivial. The most obviously trivial case seems to be that of a single species occupying a given trophic level. As opposed to what is observed with top predators, the lower trophic levels are characterized by redundancy, in particular with scavengers (see references in Naeem and Li 1997). The disappearance of a single scavenger species may have major impacts on carbon flow (Taylor et al. 2006), which is much less foreseeable than with top predators.

D'autres cas d'apparence triviale sont ceux de symbioses obligatoires, comme par exemple la symbiose bactéries-algues permettant aux algues de s'approvisionner en vitamine B_{12} et aux bactéries d'obtenir des exsudats riches en carbone (Croft et al., 2005). On pourrait également penser à des systèmes de type plante/herbivore/parasitoïde, mais à ma connaissance ce ne sont pas des cas très fréquents (si tant est qu'il y en ait) en milieu marin.

Types d'effets

Par quels mécanismes le retrait ou l'addition d'une seule espèce pourrait-il affecter la longueur d'un réseau trophique? Cela dépend de la présence d'effets top-down ou bottom-up.

Si la disparition d'un niveau trophique supérieur perturbe les effets top-down, il pourrait y avoir changement du poids relatif des différents niveaux trophiques rappelant le principe de trialité (voir Fig. 1; voir aussi Schwemmler, 1980). Si on est en présence d'effets bottom-up, la disparition d'un niveau trophique intermédiaire pourrait soit augmenter le flux d'énergie vers le haut du réseau trophique par la disparition d'une étape de transfert trophique avec les pertes respiratoires et autres qui lui sont associées, soit diminuer le flux d'énergie vers les niveaux trophiques supérieurs si l'espèce disparue était une proie essentielle aux prédateurs originaux à cause de sa taille (ou quelque autre raison que ce soit).

Aspects non couverts par la présente analyse

Nous ne touchons pas la question des *espèces envahissantes*, bien qu'elles puissent avoir des impacts importants sur la structure trophique des écosystèmes. Le cas de la moule zébrée est éloquent à ce sujet. Il faut en retenir qu'il s'agit d'un effet se produisant au bas de la chaîne trophique.

Les *parasites* ne sont pas inclus. Il semble d'ailleurs que ce soit le cas dans l'immense majorité des études, en dépit de l'importance vraisemblable de leur rôle dans les écosystèmes (Hudson et al., 2006). Finalement, les *espèces nuisibles* caractérisées par des explosions démographiques ne sont pas incluses (ex. la tordeuse du bourgeon de l'épinette).

Other cases that are trivial in appearance are those of obligatory symbiosis, such as the bacteria-algae symbiosis through which algae obtain B12 vitamin, and bacteria benefit from carbon-rich exudates (Croft et al. 2005). The same may also be true for systems involving plants, herbivorous and parasitoids, but I think these cases are scanty (in as much as there are) in marine environment.

Types of impacts

Through which mechanisms the withdrawal or addition of only one species could affect the length of a food web? That depends on the presence of top-down or bottom-up impacts.

If the disappearance of a higher trophic level disturbs the top-down impacts, there could be a change in the relative weight of the various trophic levels, as with the principle of triality (see Fig. 1; see also Schwemmler 1980). In the case of bottom-up impacts, the disappearance of an intermediate trophic level could either increase the flow of energy towards the top of the food web as a result of the loss of a trophic transfer stage, with the respiratory and other losses that are associated with this stage, or decrease the flow of energy towards the higher trophic levels if the species lost is a critical prey for original predators because of its size (or for some other reason).

Perspectives not addressed by this analysis

We do not address the issue of *invading species*, although they can have significant impacts on the trophic structure of ecosystems. The case of zebra mussel is an excellent example. It should be noted that this impact occurs at the bottom of the food chain.

Parasites are not included. In fact, it seems to be the case in the most of the studies, in spite of the probable importance of their role in ecosystems (Hudson et al. 2006). Finally, *harmful species* characterized by demographic explosions are not included (e.g. the spruce budworm).

Proprietes des Reseaux Trophiques

Longueur des réseaux trophiques

Bien qu'elles puissent être constituées de communautés de taxonomie très diversifiée, contenant un grand nombre d'espèces (Fig. 2a; Montoya et al., 2006) les chaînes trophiques sont *courtes*. On a relevé que dans 7 communautés diversifiées, 80% et 97% des espèces étaient à deux ou trois échelons les unes des autres, ce qui fait trois ou quatre niveaux trophiques au total (Williams et al. dans Montoya et al., 2006). Notons toutefois que cette façon de représenter la situation ne tient pas compte du fait qu'un petit nombre d'espèces monopolisant différents niveaux trophiques peuvent allonger les chaînes de façon disproportionnée, surtout aux niveaux supérieurs (voir Fig.3; Cohen et al., 2003). Le niveau trophique supérieur n'est donc occupé que par une seule espèce.

Redondance aux niveaux trophiques inférieurs

Les différents niveaux trophiques ne sont pas occupés par un nombre égal d'espèces. Comme nous venons de le voir, les *niveaux trophiques inférieurs sont redondants* : un grand nombre d'espèces y jouent un rôle similaire, ce qui favorise l'efficacité et la fiabilité des utilités écosystémiques assurées par ces niveaux (McGrady-Steed et al., 1997; Naeem and Li, 1997).

Compartimentation des réseaux trophiques

Les interactions entre les espèces d'un réseau trophique résultent en un certain degré de regroupement entre les espèces. Dans les réseaux caractérisés d'un grand nombre d'espèces et peu de liens par espèce, on note que le degré de regroupement est plus grand que dans des réseaux aléatoires (voir références dans Montoya et al., 2006).

L'asymétrie de la compartimentation

Dans un article récent, Rooney et al. (2006) mettent en évidence deux compartiments du flux d'énergie : une composante « lente », basée sur une chaîne trophique détritivore, et une composante « rapide », basée sur le broutage direct de matière végétale et de bactéries (Fig. 4). Cette compartimentation disparaît au niveau trophique supérieur. Le compartiment lent se caractérise par un rapport P/B faible, une

Properties of Food Webs

Length of food webs

Although they can consist of communities of very diversified taxonomy, containing a great number of species (Fig. 2a; Montoya et al. 2006) food chains are *short*. It was noted that in 7 diversified communities, 80% and 97% of the species were between two or three levels apart from each other, which totals three or four trophic levels (Williams et al. in Montoya et al. 2006). However, it should be noted that this way of representing the situation does not consider that a small number of species monopolizing various trophic levels may lengthen the chains in a disproportionate way, especially at higher levels (see Fig.3; Cohen et al. 2003). Thus, the higher trophic level is occupied by only one species.

Redundancy at lower trophic levels

The various trophic levels are not occupied by an equal number of species. As mentioned above, the *lower trophic levels are redundant*: a great number of species play a similar role, supporting the effectiveness and the reliability of the ecosystem services associated to these levels (McGrady-Steed et al. 1997, Naeem and Li 1997).

Compartmentalization of food webs

Interactions between species in a food web result in a certain degree of aggregation between these species. In webs featuring a large number of species and with few interspecies links, the degree of aggregation is larger than in random-type webs (see references in Montoya et al. 2006).

The asymmetry of compartmentalization

In a recent article, Rooney *et al.* (2006) highlighted two compartments of energy flow: a "slow" component, based on a scavenging food chain, and a "fast" component, based on direct grazing of vegetable matter and bacteria (fig. 4). This compartmentalization disappears at the higher trophic level. The slow compartment is characterized by a low P/B ratio, low total production and weak interactions. The fast

production totale faible et des interactions faibles. Le compartiment rapide se caractérise par un rapport P/B élevé, une production totale élevée et des interactions fortes. Les deux filières sont couplées par les prédateurs de haut niveau trophique. Les simulations de Rooney et al. indiquent que le caractère asymétrique de la vitesse de « turnover » des deux compartiments augmente le flux d'énergie total et la stabilité du système.

Invariance d'échelle

De plus, si on examine la probabilité $P(k)$ que les éléments de réseaux non biologiques (tels qu'internet ou les réseaux sociaux humains) aient k liens, on trouve $P(k) = a\,k^{-\gamma}$, avec $\gamma =]2,3]$. Cette fonction de puissance (on parle d'invariance d'échelle) traduit une préférence pour les éléments déjà reliés à plusieurs autres (« les riches s'enrichissent »). Dans les chaîne trophiques, on trouve plutôt $P(k) = a\,k^{-\gamma}\,e^{-k/\xi}$, avec $\gamma \approx 1$ et ξ approximativement égal au nombre moyen de liens par espèce. Le paramètre γ traduit ici aussi le fait qu'un *petit nombre d'espèces est très lié à plusieurs autres*. À ceci s'ajoute le paramètre ξ, qui traduit l'effet de contraintes qui accentuent la *compartimentation* des interactions entre les espèces (il faut toutefois noter que la question de l'invariance d'échelle fait encore objet de débat; May, 2006).

En résumé, les réseaux trophiques sont *courts*, ils sont *redondants aux niveaux inférieurs*, ils sont *compartimentés* et se terminent par un niveau à *une seule* ou peu d'espèces. Ici, on retrouve le cas trivial d'une seule espèce par niveau trophique (mais encore une fois, est-ce vraiment trivial ?).

L'identification des EIBE

En haut du réseau trophique

En principe, la compartimentation et la présence de niveaux trophiques constitués de peu d'espèces fournissent des éléments structuraux par lesquels l'addition ou le retrait d'une seule espèce ou d'un petit nombre d'espèces pourrait modifier le nombre de niveaux trophiques.

Le Tableau 1 résume les relations possibles entre le concept des EIBE et les réseaux trophiques. En résumé, les EIBE se retrouvent dans les niveaux peu redondants. Il s'agit des prédateurs de niveau supérieur. Dobson et al. (2006) citent des

compartment is characterized by a high P/B ratio, high total production and strong interactions. These two channels are coupled by predators of high trophic level. Simulations of Rooney *et al.* indicate that the asymmetrical character in the "turnover" rate of the two compartments increases the total flow of energy and the stability of the system.

Scale-free

Moreover, when examining the probability $P(k)$ that the non-biological elements of webs (such as the Internet or human social networks) have k links, we can conclude that $P(k) = a\,k^{-\gamma}$, where $\gamma =]2,3]$. This power function (referred as "scale-free") translates a preference for elements already linked to several others ("the rich become richer"). In food chains, it is $P(k) = a\,k^{-\gamma}e^{-k/\xi}$, where $\gamma \approx 1$ and ξ roughly equal to the average number of links per species. The parameter γ also translated here the fact that a *small number of species are strongly linked to several others*. In addition to this adds the parameter ξ, which translates the impact of constraints that accentuate the *compartmentalization* of the interactions between the species (however, it should be noted that the scale-free issue still raises discussion; May 2006).

In summary, food webs are *short*, *redundant at the lower levels*, *compartmentalized*, and end at a level where *only one* or few species are present. Here, it is the trivial case of a single species by trophic level (but once again, is this really trivial?).

EBSS Identification

On top of food web

In theory, the compartmentalization and the presence of trophic levels made of a few species provide structural elements by which the addition or withdrawal of only one species or a small number of species could modify the number of trophic levels.

Table 1 summarizes the possible relations between the EBSS concept and food webs. In short, EBSSs are found in the low redundancy levels. They are the predators of higher level. Dobson *et al.* (2006) give examples for both maritime fisheries (e.g. work

exemples tant pour les pêches maritimes (on pense aux travaux de Pauly et al., 1998) que pour les écosystèmes continentaux. J'en ai trouvé de nombreux autres exemples qui sont cités dans Montoya et al. (2006) et Rooney et al. (2006), que je n'ai pas cités ici parce que je n'ai pas pu les lire moi-même faute de temps.

Quelques Sources D'Erreur

Équilibres alternatifs stables et faux positifs

Un postulat implicite dans mon analyse est que les systèmes que nous avons abordés représentaient la seule configuration stable (et naturelle) des peuplements. Or ces configurations ne sont pas nécessairement les seules qui puissent exister. En effet, on peut trouver des communautés basculant d'une configuration stable à une autre sous l'effet d'agents physiques (Schröder et al., 2005). On parle alors d'états stables alternatifs des communautés. Si les différentes configurations ont des chaînes trophiques de longueur différente comme on le voit sur les littoraux rocheux du Maine (Petraitis and Dudgeon, 2005), on pourrait être tenté d'associer les niveaux trophiques supplémentaires (ou en moins) à un rôle particulier des espèces en cause dans la stabilité des communautés, alors que leur apparition ou disparition ne serait en fait qu'un épiphénomène d'un mécanisme de contrôle exogène.

Les faux négatifs

Nous avons vu que les écosystèmes sont compartimentés. Ce degré de compartimentation peut réduire l'impact apparent de la disparition d'une EIBE, puisque certains compartiments pourraient ne pas être affectés. Il en va de même pour les d'états stables alternatifs des communautés, dont les différentes configurations peuvent changer abruptement dans l'espace et coexister sur des sites de taille restreinte (Schröder et al., 2005). Une configuration pourrait être affectée par la perte d'une EIBE et cet effet pourrait n'être pas facilement perçu en raison du fait que les autres états ne seraient pas affectés, l'ensemble du peuplement ayant l'air plus ou moins stable.

of Pauly et al. 1998) and continental ecosystems. I found many other examples that are quoted in Montoya *et al.* (2006) and Rooney *et al.* (2006), but I did not quote them here because I could not read them due to a lack of time.

Some Sources of Error

Stable alternative equilibrium and false positives

An implicit postulate in my analysis is that the systems that we addressed represented the only stable (and natural) configuration of populations. But these configurations are not necessarily the only ones that may exist. In fact, communities alternating from a stable configuration to another under the effect of physical agents are found (Schröder et al. 2005). In such cases, we refer to alternative stable states of communities. If the various configurations have food chains of different length, as it can be seen on the rocky shores of Maine (Petraitis and Dudgeon 2005), we could attempt to associate the additional trophic levels (or in less) with a particular role of these species in the stability of communities, whereas their appearance or disappearance would be in fact only one epiphenomenon of an exogenic control mechanism.

False negatives

We saw that ecosystems are compartmentalized. This degree of compartmentalization can reduce the apparent impact of the disappearance of an EBSS, since certain compartments could not be affected. The same applies for alternative stable states of communities, whose various configurations can change drastically in space and coexist on sites of limited size (Schröder et al. 2005). A configuration could be affected by the loss of an EBSS, and this impact could be hardly perceived as the other state would not be affected, the whole of the community looking more or less stable.

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Tableau 1: Propriétés des réseaux trophiques et leurs conséquences possibles sur un lien entre les EIBE et la longueur des chaînes trophiques. En conclusion : les prédateurs de haut niveau trophique sont peu ou non redondants; ce sont des espèces avec des liens forts; leur disparition entraînerait des changements importants du réseau trophique, dont le changement de la longueur des chaînes trophiques. Un changement de longueur de chaîne trophique peut donc être utilisé pour identifier des EIBE : ce seront probablement des prédateurs supérieurs.

Table 1: Properties of food webs and their possible effects on a link between EBSSs and the length of the food chains. In conclusion: predators of high trophic level are little or not redundant; they are species with strong links; their disappearance would result in significant changes in the food web, including a change in the length of food chains. A change in the length of food chain can thus be used to identify EBSSs: they will be probably top predators.

propriété	conséquences possibles sur un lien entre les EIBE et la longueur des chaînes trophiques
courts	?
redondants aux niveaux inférieurs	augmente la probabilité que la disparition d'une espèce soit associée à un changement de longueur de chaîne trophique seulement si l'espèce en cause est de niveau trophique supérieur
compartimentation	augmente la difficulté d'identifier l'effet de la perte des EIBE
asymétrie de la compartimentation	compartiment rapide : interactions fortes (espèces EIBE)
	compartiment lent : interactions faibles (espèces non-EIBE)
invariance d'échelle	?

property	possible effects on a link between EBSSs and food chain length
short	?
redundant at lower levels	increase the probability that the disappearance of a species of only a higher trophic level be associated with a change in the food chain length
compartmentalization	increase the difficulty in identifying the impact of the loss of EBSSs
asymmetry of compartmentalization	fast compartment: strong interactions (EBSS species)
	slow compartment: weak interactions (non-EBSS species)
invariance of scale	?

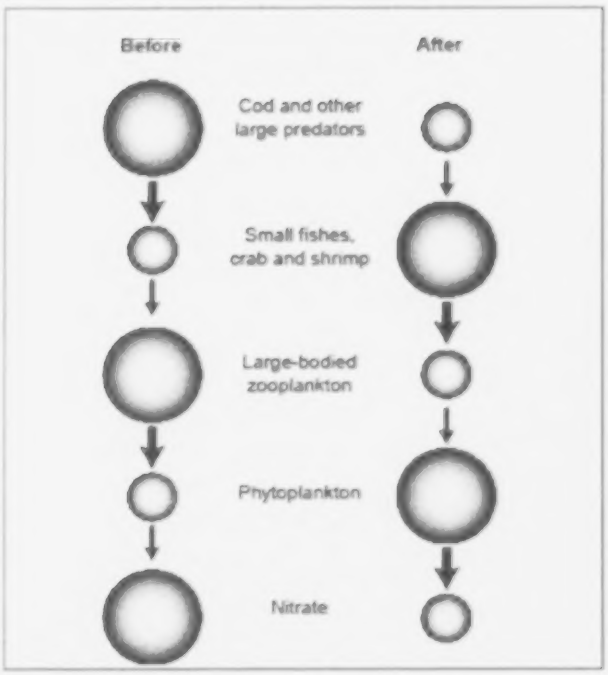

Fig. 1. Schéma de cascade trophique de l'effet de la surpêche (basé sur Frank et al. Science 308:1621-1623). Un tel effet ne se traduit pas par un changement de la longueur du réseau trophique, mais par un basculement de l'importance relative des niveaux trophiques. Tiré de Scheffer et al. (2005).

Fig. 1. Trophic cascade diagram showing the impacts of overfishing (based on Frank *et al.* Science 308:1621-1623). Such impacts do not result in a change in food web length, but cause a tipping-over in the relative importance of trophic levels. From Scheffer *et al.* (2005).

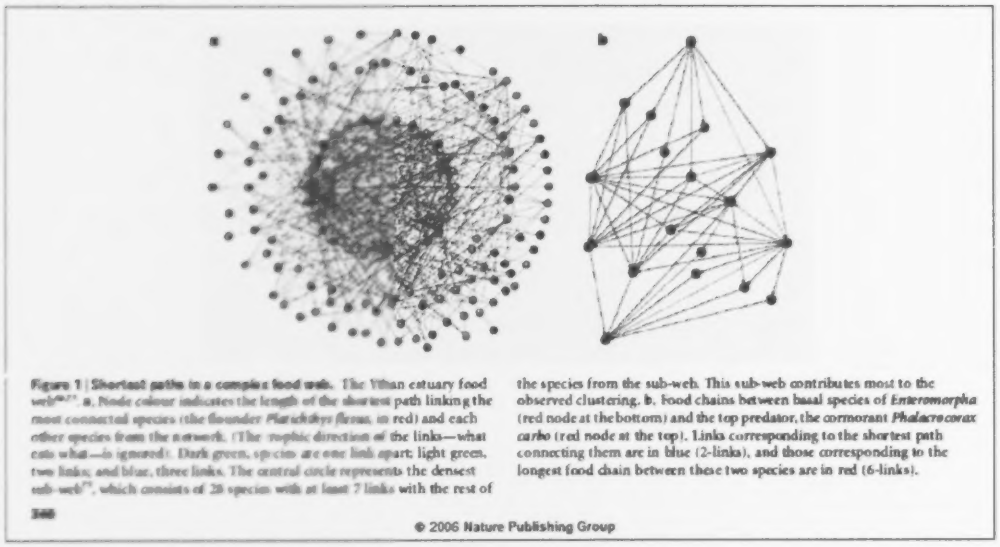

Figure 1 | Shortest paths in a complex food web. The Ythan estuary food web[26,27]. **a**, Node colour indicates the length of the shortest path linking the most connected species (the flounder *Platichthys flesus*, in red) and each other species from the network. (The trophic direction of the links—what eats what—is ignored). Dark green, species are one link apart; light green, two links; and blue, three links. The central circle represents the densest sub-web[27], which consists of 28 species with at least 7 links with the rest of the species from the sub-web. This sub-web contributes most to the observed clustering. **b**, Food chains between basal species of *Enteromorpha* (red node at the bottom) and the top predator, the cormorant *Phalacrocorax carbo* (red node at the top). Links corresponding to the shortest path connecting them are in blue (2-links), and those corresponding to the longest food chain between these two species are in red (6-links).

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Fig. 2. Schéma du réseau trophique de l'estuaire de la Ythan. Tiré de Montoya et al. (2006).

Fig. 2. Diagram of the Ythan estuary food web. From Montoya *et al.* (2006).

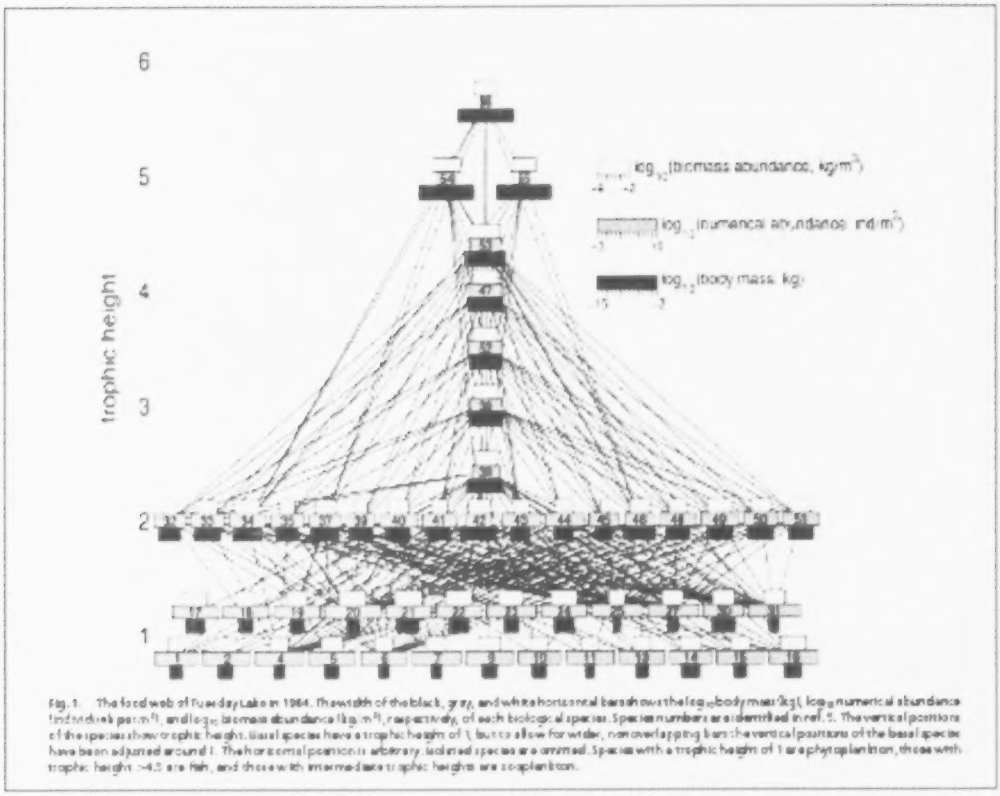

Fig. 1. The food web of Tuesday Lake in 1984. The width of the black, gray, and white horizontal bars show the $\log_{10}$ body mass (kg), $\log_{10}$ numerical abundance (individuals per m^2), and $\log_{10}$ biomass abundance (kg/m^2), respectively, of each biological species. Species numbers are identified in ref. 5. The vertical positions of the species show trophic height. Basal species have a trophic height of 1, but to allow for wider, non-overlapping bars the vertical positions of the basal species have been adjusted around 1. The horizontal position is arbitrary. Isolated species are unnamed. Species with a trophic height of 1 are phytoplankton, those with trophic height >4.5 are fish, and those with intermediate trophic heights are zooplankton.

Fig. 3. Réseau trophique de Tuesday Lake en 1984. Soulignons la diminution du niveau de redondance au fur et à mesure que l'on gagne les niveaux les plus élevés, où quelques espèces parviennent presque chacune à monopoliser un niveau trophique. Tiré de Cohen et al. (2003).

Fig. 3. Tuesday Lake food web in 1984. Note the reduction in redundancy level as the highest levels are reached, where some species almost monopolize a trophic level. From Cohen *et al.* (2003).

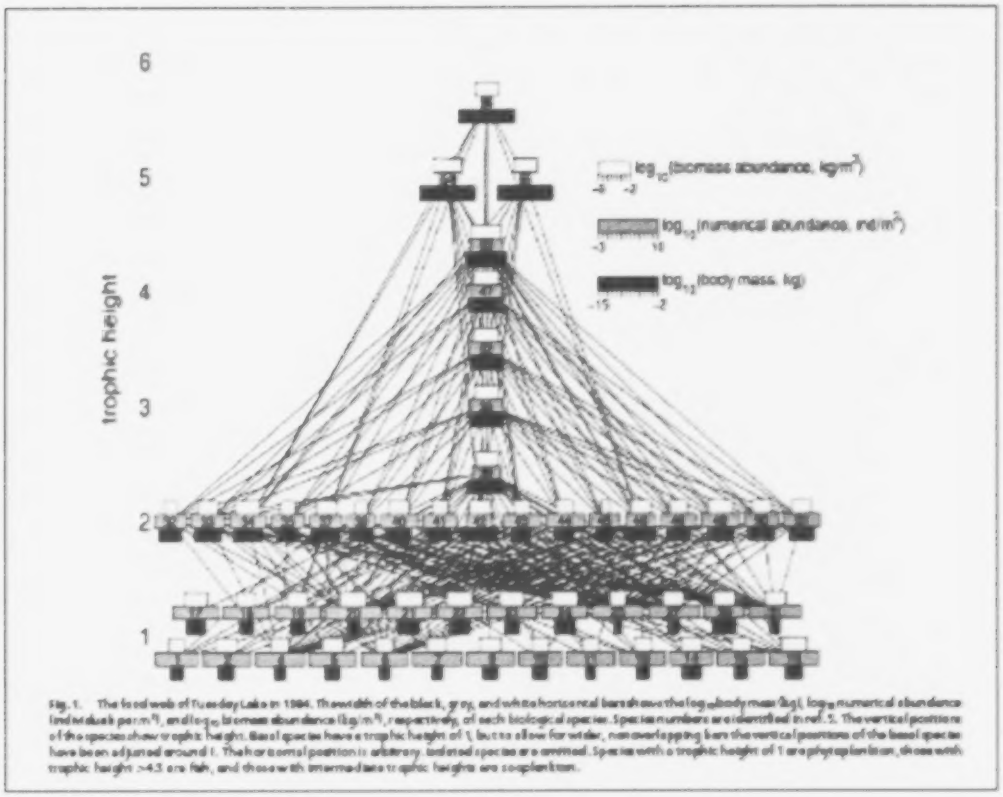

Fig. 1. The food web of Tuesday Lake in 1984. The width of the black, gray, and white horizontal bars shows the $\log_{10}$ body mass (kg), $\log_{10}$ numerical abundance (individuals per m^3), and $\log_{10}$ biomass abundance (kg/m^3), respectively, of each biological species. Species numbers are identified in ref. 5. The vertical positions of the species show trophic height. Basal species have a trophic height of 1, but to allow for wider, non-overlapping bars the vertical positions of the basal species have been adjusted around 1. The horizontal position is arbitrary. Isolated species are omnivores. Species with a trophic height of 1 are phytoplankton, those with trophic height >4.3 are fish, and those with intermediate trophic heights are zooplankton.

Fig. 3. Réseau trophique de Tuesday Lake en 1984. Soulignons la diminution du niveau de redondance au fur et à mesure que l'on gagne les niveaux les plus élevés, où quelques espèces parviennent presque chacune à monopoliser un niveau trophique. Tiré de Cohen et al. (2003).

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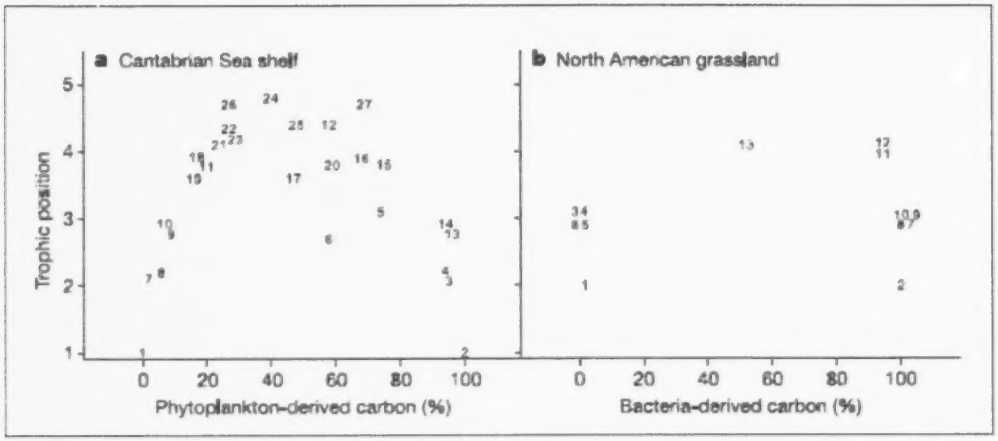

Fig. 4. Relation entre le niveau trophique (« trophic position ») et la proportion de carbone ingéré provenant du phytoplancton, par opposition au carbone détritique. Tiré de Rooney et al. (2006).

Fig. 4. Relation between trophic level ("trophic position") and proportion of carbon ingested from phytoplankton, compared to detrital carbon. From Rooney *et al.* (2006).

Resilient/Sensitive Species

Tana Worcester, Glen Jamieson and Heather Breeze

Abstract

The ecological perspective of resilience has been described as the amount of disturbance that can be absorbed or tolerated before there is a change in state or structure. Sensitivity, which is considered here as the inverse of resilience, also includes concepts of tolerance and recovery. Sensitive species can be easily depleted by some human activities and when affected, are expected to recover over a long period or not at all. It is difficult to discuss resilience/sensitivity without identifying disturbances that might be encountered, such as changes in temperature, sediment movement, physical disturbance, salinity, etc. However, some species have biological characteristics (life-history traits) that make them resilient/sensitive to a broad suite of changing environmental conditions and human impacts. These features include aspects of recruitment, recolonization, regeneration, habitat requirements, and physical structure. Characteristics and examples of sensitive species are presented.

Introduction

Definition of resilience/sensitivity

There appear to be two competing, though complementary definitions of resilience, one which has emerged from an engineering perspective and one which has evolved in the ecological literature.

1. Engineering perspective: resilience can be described as the ability or rate at which something (e.g., a species or community) returns to a steady or cyclic state following a perturbation (Pimm, 1984; O'Neill *et al.*, 1986; Tilman and Downing, 1994; Tilman, 1996). This is also referred to as "recoverability".

2. Ecological perspective: resilience can also be described as the amount of disturbance that can be absorbed or tolerated before there is a change in state or structure (Walker *et al.*, 1969; Holling, 1996; Holling, 1973). This is also referred to as "tolerance" or "resistance".

The engineering definition of resilience tends to assume the existence of one stable state from which divergence (and recovery) is measured. The ecological definition of resilience allows for the possibility of alternative stable states. Both concepts may be useful to consider within this discussion of resilience.

Sensitivity, which is considered here as the inverse of resilience, has also evolved to include concepts of tolerance and recovery (ICES, 2004; Cooke and McMath, 2001; Hiscock and Walters, 2006):

> *After some discussion and clarification, the definition of sensitivity provided as a part of the 'Texel/Faial criteria for the identification of species and habitats in need of protection' (developed by OSPAR) was adopted. Sensitive species – A species easily depleted by human activity and when affected is expected to recover over a long period or not at all. As such the term "sensitivity" takes into account both the tolerance to and the time needed for recovery (largely species dependent) from the stressor.* (ICES, 2004)

In this paper, resilience and sensitivity are used to describe the two ends of a common axis ranging from resilient to sensitive. The meeting to discuss Ecologically and Biologically Significant Species may wish to select *one* of these terms.

Resilient ----------Sensitive

Resilience in a species context

In a species context, resilience/sensitivity may be translated into an ability to withstand changes or disturbances in the environment and/or to recover from disturbance should this disturbance cease. It may be difficult to discuss resilience/sensitivity without identifying the disturbances that might be encountered, such as changes in temperature, changes in sediment movement, physical disturbance, changes in salinity, etc. However, there may be some species that have biological characteristics (life-history traits) that make them resilient/sensitive to a broad suite of changing environmental conditions and human impacts.

Community resilience: There may also be community (emergent) properties that enable ecosystems to be more resilient, such as high species richness or functional overlap, but these community level characteristics are not addressed in this paper.

Importance of resilience/sensitivity

Resilient species may help to maintain ecosystem function during periods of disturbance. This buffering function of resilient species may provide the opportunity/time needed to reduce/remove human impacts *before* irreversible harm or ecosystem shifts have occurred. Resilient species may also help to facilitate the transition between stable states during a regime shift. However, resilient species are typically those that are the least vulnerable to human activities and therefore may constitute a low conservation priority (i.e., actions may not have to be taken to protect resilient species, even if they play an important ecological role).

Sensitive species, on the other hand, tend to be species that are most vulnerable to human activities and therefore tend to constitute a high conservation priority. While sensitivity in and of itself is not necessarily a reflection of significance, sensitivity can be used as a secondary criteria for prioritization purposes.

Criteria for resilience/sensitivity

The following criteria could potentially be used for the identification of resilient/sensitive species:

- Recruitment:
  - Frequency and length of reproductive season
  - Fecundity
  - Age of maturity
  - Reproductive mechanisms (e.g., asexual vs. sexual reproduction)
  - Settlement/development success
  - Longevity

- Recolonization:
  - Mobility
  - Range

- Regeneration:
  - Regenerative capacity (rate of regeneration)
  - Growth rate

- Habitat Requirements:
  - Temperature, Salinity, Oxygen requirements
  - Physical habitat requirements (e.g., for settlement)
  - Tolerance to environmental variability

- Fragility:
  - Body size
  - Shell strength

Sensitive species may have the following characteristics:

Fragility

Species that have characteristics that make them vulnerable to physical disturbance, i.e., are easily damaged, broken or destroyed, such as soft or brittle body structures.

Habitat Requirements

Species that tolerate a narrow range of environmental parameters, such as temperature salinity and oxygen, have stringent/limited physical habitat requirements (e.g., specific habitat requirements for larval settlement, or distribution is restricted to a rare habitat type).

Recruitment

Species that have low fecundity, take a long time to mature, or have a short reproductive season.

Recolonization

Species that are not particularly mobile, have a small "home range" or are territorial, are rare, have a patchy distribution (distributed a greater distances than the typical range of the species).

Regeneration

Species that do not regenerate damaged tissue or limbs easily, if at all.

Resilient species may have the following characteristics:

Habitat Requirements

Species that can tolerate a wide range of environmental conditions (temperature, salinity, oxygen) and habitat types.

Fragility

Species with hard, protective shells.

Recruitment

Species with high fecundity, low age of maturity, or long reproductive season.

Recolonization

Species with high mobility, large ranges, or effective dispersal mechanisms.

Regeneration

Species that can regenerate tissue or limbs (e.g., starfish) or that have fast growth rates.

Nutrition

Species that have developed mechanisms that enable them to effectively process/metabolize human inputs, such as contaminants.

Examples

Sensitive Species (or low resilience)

Species that have *k* coefficients at or below 0.10 seem to be particularly vulnerable and include most elasmobranchs, most chondrichthians, some teleosts, and the cheloniid sea turtles (Musick, 1999).

Fragile species – brittle stars, soft-shelled clams, horse mussels, moulting lobsters, some coral and sponge species.

Long-lived species – some clams (quahogs and *Artica islantica* up to 100 years), corals (e.g. bamboo coral = 80-220 years), sea fans (e.g. *Eunicella verrucosa* = 40 years), marine mammals in general (e.g., orca = 70 years, grey whale = 60 years, harbour seal = 30 years), sea turtles, *Littorina* (16 years), red sea urchin (50 years). Though age of maturity might be a better indicator, e.g. *Artica islantica* = 5-11 years,

Species sensitive to low oxygen include *Diastylis rathkei* (cumacean), *Nephrops norvegicus* (decapod), *Echinarachnius parma* (echinoderm), *Ampelisca agassizi* (amphipod), *Gammarus tigrinus* (amphipod), *Spisula solida* (bivalve), *Asterias forbesii* (echinoderm), *Crangon crangon* (decapod), *Carcinus maenas* (decapod), and *Magelona phyllisae* (polychaete), etc..

Resilient Species (or low sensitivity)

Herring, anchovy, and other small pelagics with high k values may have high resilience.

Barnacles have high fecundity, a larval stage, reach sexual maturity rapidly, reproduces frequently, has high settlement success, and is known to recolonize rapidly after clearing.

Starfish (Asteroidea and Ophiuroidea) are able to rapidly replace missing limbs. Porifera are able to regenerate tissue rapidly from small fragments. Large portions of the blade of kelp can be removed and rapid regrowth can occur if the meristematic basal area of the blade remains (not *Alaria esculenta*).

Some coral species appear to have evolved mechanisms to deal with various forms of disturbance, e.g., initiate reproduction (larval expulsion) upon contact, regenerate from acute localized injuries, or increase feeding in response to bleaching.

Some clam species, e.g., quahogs, have hard shells that may protect them from limited forms of physical disturbance.

Glossary

Regeneration: Replacement by compensatory growth and differentiation of lost parts of an organism.

Resistance: The degree to which a variable is changed following perturbation. The tendency to withstand being perturbed from the equilibrium.

Fragility: Quality of being easily damaged, destroyed or broken.

Vulnerability: Susceptibility to degradation or damage from adverse factors or influences. The likelihood that a habitat, community or individual (or individual colony) of a species will be exposed to an external factor to which it is sensitive. This is similar to fragility though may include additional factors such as proximity to adverse factors.

Tolerance: The ability of an organism or biological process to subsist under a given set of environmental conditions (particularly unfavourable conditions).

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